THE UNIVERSITY *of* EDINBURGH

IMPLEMENTATION OF GENOMIC SELECTION IN UK BEEF AND SHEEP BREEDING

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To my nieces and nephews and their parents;

Ella, Sophie, Lucy, James, Lucas and Louis

Ashley, Alison, Mick and Sven

Declaration

I declare that I have composed the present thesis. This is my own work and any assistance has been duly acknowledged. The work described has not been submitted for any other degree or professional qualification.

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Publications

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Glossary of commonly used names, terms and acronyms

AI	Artificial insemination
BASCO	Limousin and Texel pedigree database and genetic evaluation provider
BCMS	British cattle movement service (database of GB cattle)
BLUP	Best linear unbiased prediction
Commercial	Herds and flocks breeding animals for slaughter (not pedigree)
Defra	UK government office responsible for agriculture
EBV	Conventional BLUP Estimated breeding value
Elite	Small core of pedigree herds or flocks driving selection with herd/flockbook
GBV	Genomic breeding value (no EBV information)
GEBV	Blend of GBV and EBV
GS	Genomic selection
MC	Male cohort (group of males born in any one year and pedigree registered in the herdbook/flockbook)
MGS	Maternal grand sire
MI	Maternal selection index
NS	Natural service (natural mating system using bulls or rams)
PGS	Paternal grand sire
Prime	Prime cattle or sheep are those bred for slaughter at a relatively young age (<30 months old in cattle and <7 months old in sheep) in commercial herds and flocks
QTL	Quantitative trait loci
Signet	Breeding entity of EBLEX (industry levy body)
Suckler	Commercial cow rearing calves by suckling
SNP	Single nucleotide polymorphism
TI	Terminal selection index (Beef and Sheep)

Abstract

Genomic selection (GS) has been adopted by the dairy cattle breeding industry and the opportunity exists to implement this technology in UK beef and sheep breeding. However, these sectors do not appear so readily predisposed to GS implementation. Following an introduction to GS in Chapter 1, Chapter 2 investigated the structure of the little-studied UK beef breeding sector. This provided estimates of key commercial and pedigree population parameters, for use in modelling genetic gain from GS. Terminal traits were found to be the dominant selection goals, with 85% of beef-sired commercial matings resulting in progeny being slaughtered at a prime age. Pedigree bulls disseminated the majority of genes in the sector via natural service. The correlation between the terminal selection index (TI) and the sale price of breeding bulls was moderate, suggesting a modest uptake of genetic technology in the sector. Chapter 3 estimated selection intensity for TI, generation interval and the dissemination rate of improved genes in the pedigree Limousin population. In order to predict the genetic gain achievable in using GS in beef and sheep breeding, Chapters 4 to 6 undertook deterministic selection index simulations, incorporating genomic information as correlated traits. In Chapter 4, GS was modelled for terminal beef traits, when incorporating carcass information and accounting for likely genotype by environment interaction. Using a training population of 2000 sires, this concept was predicted to offer 40% greater genetic gain than existing BLUP selection using pedigree phenotypes. Gene flow methodology projected the commercial value of this gain to offer a substantial return net of genotyping costs. Chapter 5 explored GS for maternal beef traits within the concept of a nucleus breeding scheme. Whilst greater genetic gain was predicted with GS than with conventional BLUP, the economic value of this gain was projected to be too low to justify such a scheme in the UK. Chapter 6 proposed a synergy between computer tomography (CT) phenotypes and GS in sheep breeding. Developing a genomic

predictor from male selection candidates with CT phenotypes and conventional performance records was predicted to increase genetic gain by 55% over BLUP selection without CT traits. Introducing GBV contributed most of the accuracy in this scenario, suggesting that the existing performance recording structure in UK sheep breeding could in the future be replaced by GS using CT. In the general discussion, the potential for GS in other beef and sheep traits was considered in the light of the outcomes of these simulations. Given the lack of vertical integration in UK beef and sheep sectors, the drivers for implementation of GS are examined. Finally, the options for international cooperation and the possibilities offered by future genotyping technology are considered. It was concluded that implementation of GS incorporating beef carcass phenotypes was merited and could provide a platform for future GS implementation in other novel traits. Sheep GS with CT traits was considered a higher risk strategy, due to the lack of evidence for uptake of existing EBV technology.

Chapter 1:

General Introduction

1.1. Towards genomic selection in cattle and sheep

The estimation of genetic merit in farmed livestock is not new. Whether consciously understood or otherwise, judging the breeding merit of animals by appearance, pedigree, or empirical measure all constitute an attempt at assessing the quality of characters which may be passed on to offspring. Effectively, using these clues in selecting breeding animals constitutes an estimation of the underlying genetic makeup of the animal. In recent years, statistical genetic techniques have allowed this estimation to gain considerable precision, but still without actually knowing the underlying genetic code. This has been achieved mathematically, using selection index methodology and linear mixed models, by decomposing the phenotype into its genetic and environmental components. In doing so, estimated breeding values (EBV), reflecting additive genetic merit, can be calculated for individual breeding animals. The application of Henderson's Best Linear Unbiased Prediction (BLUP) in estimating EBV (Henderson, 1975) became the widely adopted method of quantifying genetic variance in the twentieth century. This method uses knowledge of the pedigree relationships between animals in order to accurately weight information from relatives for estimation of breeding values. However, this method cannot distinguish between full sibs at the newborn stage and therefore attributes equal EBV to these animals. Considerable genetic improvement in economically important traits of farmed species has been achieved in the twentieth century using BLUP, notably in poultry, pigs and dairy cattle (Smith 1984; Simm *et al.* 2004). Whilst this 'black box' approach (Hill, 2010) has proven successful in quantitative trait selection, research has nevertheless continued into developing an understanding of the underlying genetic mechanisms governing these traits.

1.1.2. QTL and single gene selection.

Towards the end of the twentieth century, progress in genotyping technology enabled livestock selection based on the use of actual DNA information. Quantitative trait loci (QTL), thus became a target in animal breeding, and could refer to either an actual known gene location or less precisely, a region of a chromosome associated with a metric effect on a measured trait (Hill, 2010). A number of causal mutations of relatively large effect have been identified and accurately mapped to specific chromosomal locations. The myostatin gene was the first identified as such a loci in beef cattle (Charlier *et al*. 1995). Specific molecular mutations in this gene have been accurately mapped; such as Q204X in Belgian Blue and Charolais (Grobet *et al*. 1998), and more recently F94L in Limousin (Sellick *et al*. 2007). The Callypege locus in sheep was similarly found to have a major effect on muscularity (Cockett *et al*. 1994). However, a complicated inheritance and deleterious effect on meat quality reduced the potential for selection, in comparison with myostatin. These type of mutations can therefore be selected for by directly genotyping the relevant alleles in selection candidates, and this method is commonly referred to as gene assisted selection (GAS) (Villanueva *et al*. 2002).

1.1.3. Marker assisted selection.

Another use of the technology, marker assisted selection (MAS), did not rely on mapping the location of the actual mutation. Rather, MAS used the genotype of (typically) microsatellite markers in linkage disequilibrium (LD) with the mutation to predict the additive genetic effect of that QTL. MAS selection was therefore susceptible to error associated with the hidden breakdown of LD between the marker and causative mutation in selection (Haley and Visscher, 1998). Furthermore it was computationally difficult (particularly at the time) to include QTL

explaining only a small part of the total genetic variance in breeding value calculations (Daetwyler, 2009).

1.1.4. Limited use.

Fundamentally, the major drawback of both GAS and MAS was that the use of individual or a small number of genes or QTL did not result in the explanation of enough genetic variance in key production traits to greatly progress genetic improvement, and hence justify the effort of including these effects in evaluations (Calus, 2009; Goddard and Hayes, 2009). This is essentially due to the polygenic nature of quantitative traits, which are thought to be affected by hundreds or perhaps thousands of genes (Hill, 2010). Consequently these genes or markers were generally used as a first step in breeding schemes to narrow down selection candidates, such as the use of mutations in the DGAT1 milk fat gene in dairy bull progeny testing in artificial insemination (AI) schemes (Misztal, 2006). Selected bulls were then still subjected to a conventional progeny test before mass marketing of their semen, and as such there was no reduction in the lengthy timescale involved in the bull proving process. Uptake of this technology was even less impacting in beef and sheep sectors, largely due to problems in validating QTL effects claimed by commercial companies marketing genetic tests (Mistzal 2006; Van Eenennaam *et al.* 2007). Furthermore, mutations of large economic effect, such as the myostatin variants, were likely to be already present in high frequency within target populations, therefore reducing the value in genotyping selection candidates.

1.1.4. Breakthrough.

With GAS and MAS achieving only a limited impact on animal breeding, research focussed on including large numbers of QTL in breeding value estimation in order to progress DNA based selection (Haley and Visscher, 1998). Once again, black box

methodology leapt ahead of molecular genetics with the publication of Meuwissen *et al*. (2001). This visionary paper catalysed a breeding revolution by proposing statistical methodologies (G-BLUP, Bayes A and 'B) to predict 'genomic' breeding values (GBV) by simultaneously estimating the effects on a particular trait of all the QTL in the genome, through a dense marker approach. Importantly, Meuwissen's concept overcame the need to accurately predict the effect of individual QTL, and relied on a good prediction of total additive genetic variance (Calus, 2009). Whist microsatellites were the genetic marker in use when this paper was published; the methodology was equally applicable to single nucleotide polymorphisms (SNP). The new science of 'genomic selection' (GS) was thus born.

1.2. Genomic Selection

Cattle and sheep have approximately 3 billion nucleotide base pairs in genomes consisting of 29 pairs of autosomal chromosomes in cattle and 26 in sheep (Maddox and Cocket, 2007; The Bovine HapMap Consortium *et al*. 2009). Only a small percentage of these bases typically display variation between any two individuals, and are thus referred to as SNP. The Bovine Hap map consortium calculated that Angus cattle have about 1 SNP every 285th nucleotide, which would imply that around 10 million are present in the Angus genome. This must be considered an approximation as clearly a large proportion of animals in the population would have to be sequenced for this to be considered an accurate estimate.

GS theory assumes that each QTL is in Linkage disequilibrium (LD) with at least one SNP marker (Solberg *et al.* 2008). The inheritance of a particular allele, associated with a quantitative trait of interest, can therefore be predicted from the inheritance of a set of SNP. The effectiveness of GS is thus assumed to be related to the extent of LD in a particular population (Calus, 2009). Selection of cattle and sheep in

agricultural breeding has tended to greatly reduce the gene pool of domesticated breeds and thus increase the extent of LD (De Roos et al**.** 2009).

One of the determinants of LD within livestock breeds is effective population size (Ne), with low Ne values generally associated with high LD (Goddard and Hayes, 2009). Ne estimates in cattle and sheep range from around 50 in Holstein-Friesian to several hundred in less genetically diverse breeds (Goddard and Hayes, 2009). This compares for example with the Ne of the Human population which is generally estimated to number between 3000 and 10,000 (Tenesa *et al.* 2007). Ne is therefore a useful parameter when estimating the likely success of GS in a given cattle or sheep breed.

1.2.1. **SNP genotyping panels.**

As most quantitative livestock traits are influenced by the effects of many QTL, the development of dense SNP marker panels has allowed an estimation of all the QTL affecting a particular trait. Genotyping panels currently in use can typically genotype approximately 800,000 SNP. In order to estimate the effect of SNP genotypes on livestock traits, it is necessary to obtain relevant phenotypes for a group of genotyped individuals. This 'training' population (TP) therefore serves as a template with which to estimate SNP effects on traits of interest and thus develop a genomic predictor. This predictor is then used to estimate the genetic merit of other animals in the general population for those traits, through genotyping alone. The accuracy of genomic prediction is mainly determined by the heritability of the trait and the number of individuals included the training population (Daetwyler, 2009). The greater both these parameters are, the better the prediction accuracy achieved.

1.2.1. GBV

The effect of all SNP on the trait of interest are simultaneously quantified using linear mixed models, producing GBV, which are sometimes also referred to as direct genomic values (DGV). An advantage of GBV over conventional BLUP breeding values is that they estimate the Mendelian Sampling Term at birth, which importantly accounts for approximately 50% of additive genetic variance. This enables genetic merit differences between full siblings to be established before they obtain individual or and/or progeny phenotypic records for the majority of economically valuable traits. In comparison, the calculation of conventional EBV assumes zero difference between full siblings in the absence of phenotypic records. As well as providing young animals with more accurate breeding values, it is suggested that GS can also reduce inbreeding in managed populations under selection (Daetwyler *et al*. 2007; Dekkers, 2007a), compared with BLUP which promotes co-selection of sib-families.

1.2.2. Combining genomic and phenotypic information

GBV and EBV information can be combined into GEBV, to make optimum use of both genomic and phenotypic information, when the marker information does not capture all the genetic variance (Dekkers, 2007 a). In this case EBV and GBV are estimated separately and then 'blended' into GEBV. Early genomic evaluations adopted this multi-step procedure; however Misztal *et al*. (2009) suggest the process can be made more accurate with a one step procedure.

1.3. Genomic selection implementation in dairy

In dairy cattle, rather than use actual phenotypes for the development of training populations, it has proved more advantageous to use de-regressed breeding values (Mrode, 2005) of AI bulls with EBV of high reliability (i.e. typically over 90%). This

process effectively produces phenotypes with heritabilities approaching 1, which are therefore ideal for accurate prediction of GBV. With the majority of breeding and commercial populations made up of pure Holstein-Friesian cattle, it has been relatively straightforward and relevant to establish within-breed genomic evaluation in the dairy sector. Large AI companies quickly latched onto the concept, sensing an opportunity to reduce the lengthy timescale involved in progeny testing elite sires, as well as the numbers of AI selection candidates required (Schaeffer, 2006). Importantly, GS has been a relatively low-risk venture for these companies. Genotyping costs are low compared with the value of AI bulls, and genomic proofs can be validated by existing progeny testing programmes. The advent of GBV has allowed young selection candidate bulls, which previously had breeding values based only on parent average with consequently low reliability in key traits (typically less than 0.4), to be genotyped and attributed GEBV (GBV plus sire EBV information) values with reliability around 0.7 (Wiggans *et al*. 2011).This level of achieved reliability proved a pivotal turning point for an industry previously reluctant to use non-progeny proven bulls. Crucially, semen from young sires with GEBV, but no progeny, gained widespread commercial acceptance and AI companies were able to achieve considerable semen sales. Hoards Dairyman (2011) reports that 'genomic bulls' (i.e. without daughter proofs) made up 58% of semen sales in Canada. Holstein International (2012) further reports that the comparable figure in the USA is approaching 50%. This demonstrates the remarkable rate of uptake of genomic technology in dairy breeding, with this product only being available in the last five years. AI companies have therefore found a way of greatly reducing generation interval in sire development (by around 3 years), whilst at the same time producing a desirable product for their consumers. Clearly, those AI companies involved in initial genomic consortia (Wiggans, 2011) gained competitive advantage over rivals and these same companies have largely driven the implementation of GS

in dairy breeding. In the longer term, however, genomics may empower individual breeders, able to obtain GBV and market semen from young bulls without involvement from those large AI companies. It is therefore too early to predict the long term effect of genomics on dairy breeding structures.

1.3.1. In summary, five important factors have driven the implementation of GS in dairy breeding;

1) The omnipotence of the Holstein-Friesian in elite and commercial breeding, and in particular the low Ne of this breed which makes for accurate GBV estimation.

2) The large influence of AI in the dairy breeding, which has provided ready-made and cost-effective TP, ready-made validation of genomic technology via existing progeny testing structures and an ability to quickly disseminate the benefits of GS widely to the commercial sector.

3) The existing dairy genetic evaluation infrastructure, with established international collaboration, which has facilitated genomic evaluations.

4) The ability of genomic technology to substantially increase the reliability, typically by 30 percentage points, of breeding values of young bulls for key traits.

5) Strong commercial demand for semen from young, non-progeny proven 'genomic' sires.

The success of GS in the dairy sector has vividly highlighted the potential of genomics to the rest of the animal breeding world, and other livestock sectors have inevitably had to consider if GS could offer benefits in their field.

1.4. The potential for implementation of GS in UK beef and sheep

Whilst Holstein-Friesian dairy breeding is ideally suited to GS, the UK beef and sheep sectors do not appear to have structures so readily predisposed to GS implementation, particularly considering points 1 and 2 above. Therefore, five key structural issues in particular, are identified below which will need to be considered when assessing the potential for GS implementation in these sectors.

1.4.1. **Genetic composition**

In contrast to dairy, beef and sheep breeders utilise a diverse range of pure breeds in seedstock herds and flocks, whilst commercial stock are typically cross-bred (Pollott and Stone 2006; Garrick, 2011). Beef and sheep breeds are also estimated to typically have larger Ne than the Holstein-Friesian population (The Bovine HapMap Consortium *et al*. 2009; Kijas *et al*. 2012). It is therefore likely that larger TP will be needed to achieve good genomic predictions in beef and dairy and these may need to be linked to the admixed commercial populations for effective selection.

1.4.2. **Breeding sector structure**

The UK has somewhat uncommon beef and sheep breeding structures by international standards; with the traditional use of beef x dairy suckler cows (Lowman, 1997), and the geographical stratification of sheep breeding (Pollott and Stone, 2006). Whilst breed use in the UK commercial sheep sector has recently been studied in detail (Pollott and Stone 2006), the breed make-up of commercial beef populations remains unclear. The impact GS can make with such livestock breeding structures has yet to be established.

1.4.3. **Breeding method**

Artificial insemination (AI) is not widely practiced in commercial beef or sheep breeding, with natural service (NS) being the reproductive method of choice (Amer, 2007). The main driving force behind GS implementation in dairy does not therefore currently exist in beef and sheep breeding. As such ready-made TP of large numbers of AI sires with high accuracy EBV will not exist in these latter sectors. Furthermore, with NS males already used from a young age (and the limited number of AI bulls and rams which are used), the scope for generation interval savings seems less clear.

1.4.4. **Uptake of Genetic technology**

Evidence for uptake of existing EBV technology by beef and sheep breeders in the UK is limited. The extent to which selection decisions are based on this technology is unclear. Many breeders still appear to base selection decisions mainly on traditional visual appraisal (Amer et al, 2007). Additionally, the extent and rate of dissemination of improved genetics to commercial beef and sheep sectors has not been recently studied in the UK. Promisingly, the UK sheep industry has experienced DNA selection when attempting to eliminate susceptible Scrapie genotypes in breeding flocks, and this scheme has been widely adopted by breeders (Dawson et al 2008).

1.4.5. **Lack of relevant phenotypes**

Beef and sheep performance recording in the UK is limited to elite pedigree herds and flocks. Currently there is no collection of phenotypes from commercial animals for use in genetic evaluation. As such, the genetic performance of breeding animals in the commercial sector is largely unknown. A national cattle database does exist in the form of British Cattle Movement Service (BCMS, 2009), although this was

designed for disease monitoring and its scope for use in beef breeding evaluation and research is unclear. Collection of sheep phenotypes is further complicated by a traditional lack of individual animal identification.

1.5. **Outline of Thesis**

The aim of this PhD is therefore to consider the scope for implementation of GS, the most powerful statistical genetic tool yet conceived for animal breeding, within the context of these structural issues described, in UK beef and sheep breeding. The study will focus on further understanding and characterising the existing industry structures, with a view to providing detailed information for an objective assessment of the potential genetic gain and consequent economic benefits achievable from GS implementation.

Chapter 2 provides an in-depth structural overview of commercial UK beef breeding, aimed at matching the information known about sheep from Pollott and Stone (2006). In particular, the breed make-up, numbers of breeding animals per breed, replacement rates, breed contribution to slaughter and maternal populations are examined. The continued influence of dairy genetics in commercial beef breeding is also investigated. In an attempt to quantify the uptake of genetic technology, a study of sale prices of young beef bulls intended for breeding, compared with their selection index values, is undertaken.

Chapter 3 examines the breeding structure of the most influential pedigree beef breed in Chapter 2, the Limousin. Selection intensity and genetic gain for existing selection indices are estimated. This chapter also complements Chapter 2 in

developing an understanding of dissemination of improved genetics, by studying the influence of large bull breeding herds within the UK Limousin Herdbook.

Chapter 4 incorporates information from the first two chapters in a deterministic selection index model used to predict the effects of GS in terminal beef traits. This model simulates the combination of GS with existing and novel commercial carcass traits and aims to account for likely genotype-environment interaction. Gene flow methodology is used to predict the commercial value of genetic gain predicted.

Chapter 5 investigates whether GS can provide a new avenue for selection of beef maternal traits, which are regarded as a problematic goal in current UK beef breeding. In this chapter, it will be considered whether GS combined with structural change in breeding practices, can offer increased genetic and economic gain to beef breeders.

Chapter 6 applies lessons from Chapters 3-5 to the UK sheep sector. The UK's most influential terminal sire breed, the Texel, is used to model the effects of GS when incorporating Computer Tomography (CT) phenotypes for selection candidates.

Chapter 7 is the general discussion which focuses on four main areas; Firstly, a brief review of key technologies and parameters affecting GS (Artificial insemination, the Bulmer effect and Inbreeding), secondly the drivers of implementation of genetic technology in UK beef and sheep breeding are discussed, thirdly a summary of the potential for GS in traits not included in Chapters 3-6 and fourthly futures possibilities of genomic selection including international cooperation and across-

breed prediction are considered. Finally conclusions and recommendations for industry are given.

Chapter 2:

Breeding structure of the UK national beef population

2.1. Introduction

The UK has a long standing tradition of beef breeding. Once considered 'the stock yard of the world' (MLC, 2007; Gibbs *et al.* 2009) and a leading exporter of seedstock cattle during the first half of the 20th century (Hall and Clutton-Brock, 1989), the UK's beef breeding sector has recently undergone much upheaval. Serious disease epidemics such as BSE, volatile meat prices and the introduction of the single farm payment have made for a turbulent period for British beef cattle breeders (Lowman, 1998: Riddell, 2005). On the positive side, the 1990's also saw the introduction of BLUP based genetic evaluation which has given breeders a powerful and objective tool to aid genetic improvement (Amer *et al*. 1998). Correspondingly, the rate of genetic gain in key traits has seen an increase since the implementation of BLUP (Amer *et al*. 2007). Yet, in 2010, beef production remains a secondary enterprise on many farm holdings (Lowman, 1998; Defra, 2008a), with an average herd size of just 28, and profitability is largely dependant on subsidy support (Riddell, 2005; Defra, 2008b).

This Chapter therefore aims to provide a detailed structural analysis of the UK beef breeding industry. This is intended to provide key parameters for use in modelling the potential of genomic selection (GS) in UK beef cattle breeding, which will be investigated in Chapters 4 and 5 of this Thesis.

2.1.1. Pedigree breeding

Elite beef cattle breeding in the UK has historically been the domain of pedigree breeders, who registered cattle within the appropriate breed herdbooks. This breeding model has remained relatively constant over time, with a small number of 'bull breeding' herds driving much of the selection within particular breeds (Ozkutuk

and Bichard, 1977; Allen, 1990). Artificial insemination (AI) has more recently facilitated the wider dissemination of genes from the most popular bulls within these herds (Keeble, 2004).

In contrast, breed use has changed dramatically in recent decades. The 1960's and 70's saw the importation of European beef breeds such as Charolais, Limousin and Simmental (Hall and Clutton-Brock, 1989). Up until then, only native British beef breeds were in use. In 1968/9, Hereford and Aberdeen Angus bulls accounted for 61% and 18% respectively of beef breeding bull licenses issued by the Ministry of Agriculture (a practice no longer undertaken), with the only non-native breed in use, the Charolais accounting for less than 1% of bull licenses at this time (Craven and Kilkenny, 1976). These breeds were targeted in the search for new genetics which could produce faster growing and later maturing cattle to meet consumer demand for leaner beef (Allen, 1990) and their introduction effectively constituted the onset of an industry-wide breed substitution event. Their importation was subject to the formation of UK herdbooks, and thus these new breeds were assimilated into the traditional breeding framework (Edwards *et al.* 1966; MAFF, 1997). Such was their popularity that, by the 1980's they had largely usurped the traditional British breeds in UK beef production systems (Allen, 1990; MLC, 1990; Pullar, 1998).

2.1.2. Commercial cross-breeding

Bulls from pedigree herds have traditionally been used to mate with cross-bred 'suckler' females (Lowman, 1997) to produce slaughter animals. Suckler females are those which rear their calf through to weaning, compared with dairy cows which have their calf removed within 48 hours for artificial rearing.

The UK suckler herd has, by international standards, an uncommon breeding structure with large numbers of replacement suckler females sourced from beef cross-breds born in dairy herds (Lowman, 1997). These cross-breds are mostly a

by-product of dairy farmers making matings in excess of replacement needs to beef bulls to increase the value of by-product calves (Southgate *et al.* 1982; Simm, 1998). This beef x dairy mating strategy was seen as a complementary mating of a dairy cow with reasonable beefing qualities to a more specialised beef terminal sire (Southgate *et al.* 1982). Thus, the adoption of cross-breeding in the suckler herd was born as much by opportunism over the availability of dairy cross-breds with advantageous additive genetic qualities as any particular drive to impart hybrid vigour into suckler beef breeding systems (Lowman, B.G, personal communication, 2010). The quantitative map of the gene flow of genetics from the dairy herd into the beef herd is summarised in Figure 2.1 (this Figure also contains results which will be discussed later in the Chapter), demonstrating the interplay between the dairy and beef herds in UK prime beef production. Throughout the following text, genetic groups such as beef, dairy and their crosses will make use of abbreviations B,D and combinations such as B x D. Here B x D refers to an animal that has a beef sire and a dairy maternal grandsire (MGS) and other crosses are defined analogously. In this context the suckler herd is defined as a B x B and B x D breeding females, and the dairy herd as D x D breeding females.

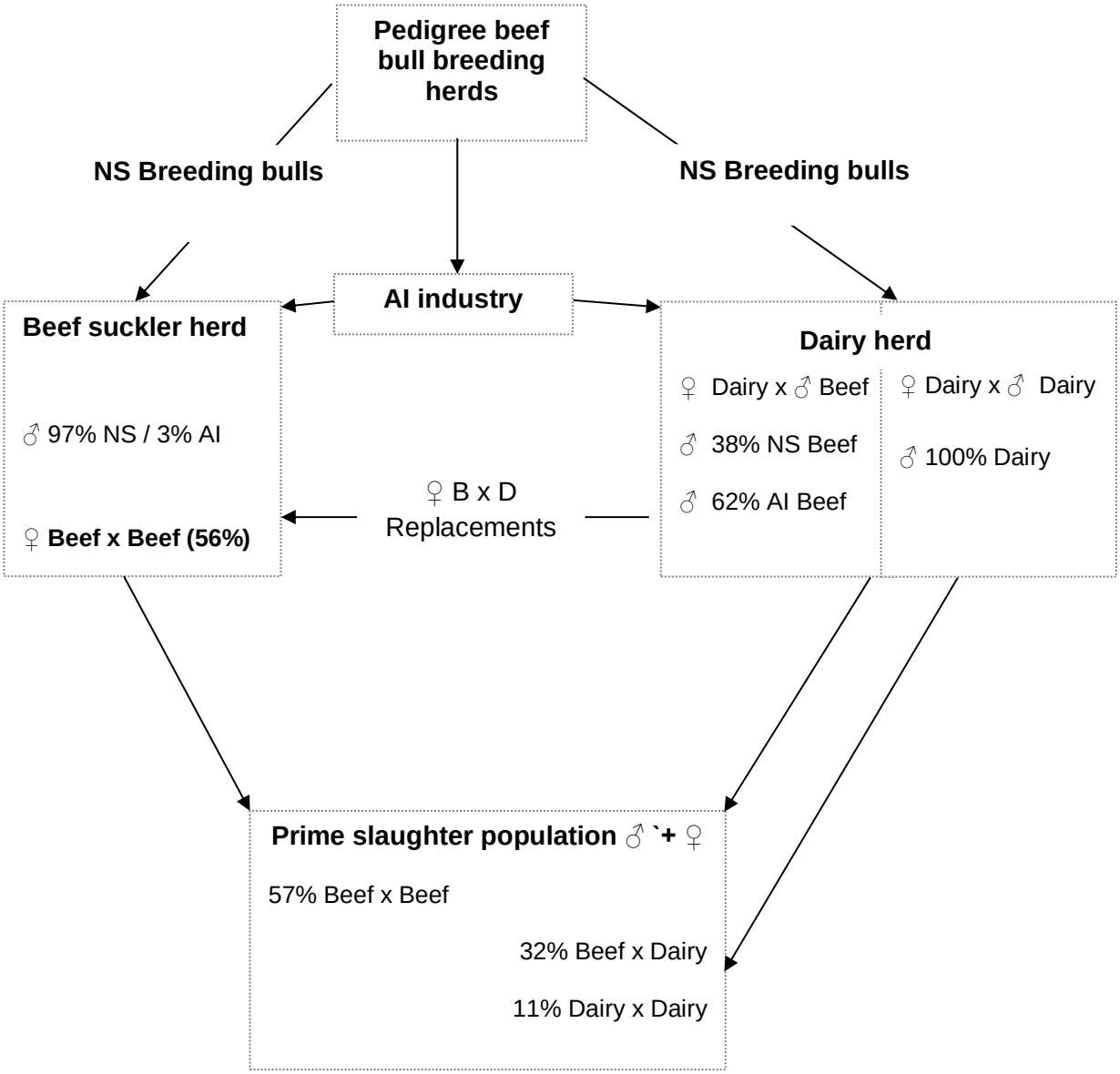

Figure 2.1 Overview of the gene flow in the UK beef population highlighting proportions of natural service (NS) and artificial insemination (AI), as well as proportions of beef (B) x dairy (D) suckler females, and proportions of beef and dairy in the prime slaughter population (based on sire and MGS from 2007/2008 BCMS/SAC).

2.1.3. Prime beef

The main aim of the UK beef industry is to produce the 'prime' animal. Traditionally this referred to an animal slaughtered at approximately less than three years of age. However, the UK BSE epidemic of the 1990's saw the introduction of a specific age at slaughter restriction of 30 months or less, with meat from cattle aged over thirty months at slaughter banned from entering the human food chain between 1996 and 2006 (Defra, 2006). The prime animal thus became rigidly defined as one aged up to 30 months of age at slaughter. Even after the removal of over thirty month restrictions, a significant market premium remains for carcasses from under thirty one month cattle.

2.1.4. Genetic evaluation. In the absence of dedicated large scale beef cattle breeding companies, a partnership between breed societies and MLC/Signet facilitated the implementation of a BLUP based genetic evaluation in pedigree herds. ABRI from Australia now also provide this service to some UK based breed societies. Genetic links from common ancestors across pedigree herds has allowed the calculation of BLUP estimated breeding values (EBV) that are comparable across the whole breed. These links were in large part achieved through the relatively high use of AI in pedigree herds (compared with commercial suckler herds), which remains at around 25% in the Limousin breed for example (Keeble, 2004). Selection of terminal sires is driven largely by lean meat yield traits, such as growth rate, muscling and fat depth. Whilst the Signet Beef Value selection index is a good predictor of grading under the EUROP carcass classification system (Simm, 1998), genetic correlations with calving and maternal traits tend to be negative. Eriksson *et al.* (2004) found higher EUROP carcass conformation to be negatively correlated with calving ease, whilst Roughsedge *et al.* (2005) found that higher 400 day weight was negatively correlated with age at first calving.

Furthermore, every major UK beef breed has seen a deterioration in genetic trends for calving ease since evaluation of this trait was first introduced in 1997 (BASCO, 2010; Breedplan 2010). This evidence for terminal and maternal/calving selection goals being antagonistic in beef cattle breeding makes selection for dual purpose goals more problematic without careful use of economic selection index methodology. Therefore, the preferential selection for terminal beef traits has seen deterioration in calving traits in all recorded pedigree beef breeds. In order to address this issue, certain breeds have incorporated calving traits into global selection indices. The genetic gain in growth and carcass traits has, however, been modest in comparison with other livestock species with more intensive production systems (Simm *et al*, 2004).

Although the introduction of EBV technology in UK in the mid 1990's has seen an improvement in the rate of gain in certain traits in elite pedigree populations, there has been no objective study of the influence of improved genetics on commercial bull buying decisions.

The combination of a somewhat marginalised, economically volatile sector with a traditional structure is reflected also in the low volume of research that has taken place, resulting in relatively poor knowledge of basic industry statistics. Application of new technologies such as genomic selection will rely on accurate predictions of potential benefits in order to gain acceptance and funding for their implementation. The uncommon breeding structure described above infers that the pathway to implementation will be different from that of other beef breeding countries. The objective of this study was therefore to produce an extensive profile of the UK's beef breeding sector using existing information sources, in terms of breed composition, genetic resource use and commercial uptake of EBV technology. Such a profile could provide the groundwork for evaluation of the potential benefits of genomic selection.

2.2. Materials and methodology

An important source of data, the British Cattle Movement Service (BCMS), was established in 1996**,** in the wake of the BSE crisis, to trace cattle births, deaths and movements using CTS (the Cattle Tracing System). In this study the data was obtained from the Scottish Agricultural College's restricted version which will be referred to as BCMS/SAC in this report. This study used all BCMS/SAC records for cattle in Great Britain (GB; comprising England, Wales and Scotland) whose death was recorded by BCMS between 1996 and 2008 inclusive, and extracted the following data for each animal: UK registration number, sex, year of birth, age at death in months, breed code, dam identification and maternal breed code.

2.2.1. Defra Farm Surveys and Slaughter Censuses

Information from Defra censuses and slaughter surveys was used to triangulate with the BCMS/SAC records to enable a cross referenced UK breed composition profile to be established. The Defra cattle census was collated annually from UK regional agricultural surveys until 2004. After this date, English and Welsh data was obtained from the BCMS records, but Scottish and Northern Irish data remained based upon their respective agricultural surveys. As such, pre and post 2004 survey results were not necessarily directly comparable. Furthermore, the level of detail in English and Welsh surveys was reduced, including for example, mature bull numbers were omitted which are important to this study. Therefore only pre-2004 cattle survey numbers were used in this study.

2.2.2. Reconciliation of BCMS/SAC and Defra Farm Surveys and Slaughter Censuses.

Due to the nature of the BCMS/SAC data and the availability of Defra slaughter records, the most reliable starting point for the industry profile was the prime slaughter population which yielded a relatively representative dataset to establish breed proportions. Since BCMS/SAC records were of dead animals, the GB slaughter population was completely represented in this data set.

Defra slaughter surveys, compiled monthly from United Kingdom (UK) slaughterhouses, recorded prime cattle in three categories only; bulls, steers or heifers, and recorded adult cattle in two categories only; cows and bulls. Thus no breed information was included in these statistics, and in order to establish the genetic makeup of these cattle, the BCMS/SAC records were analysed to determine breed composition. Since BCMS/SAC covers only GB, and Defra surveys cover the entire UK, which is GB plus Northern Ireland (NI), and the proportions of beef and dairy cattle differs between GB and NI, an adjustment was necessary to reconcile these data. According to the 2003 Defra census, 50.7% of NI breeding cattle were in the beef herd compared with 43.6% in GB. Given that 15% of the total 2003 UK breeding cattle population was in NI, the UK total beef proportion was 44.6%. The BCMS/SAC proportion of prime cattle with dairy dams was therefore reduced by a factor of 0.98 (43.6/44.6).

A further adjustment to the BCMS/SAC proportion of prime cattle with dairy dams was needed, due to the fact that a prime animal record including breed of dam would only appear if the dam's death had also been recorded by 2008. BCMS/SAC only included records of animals registered as dead in BCMS and each individual animal record only included the animal identification number of its dam and no other dam information such as breed code. Therefore only 755,000 (out of a total of 1.7 million) animals whose dam was also recorded as dead in BCMS were included in

the prime slaughter analysis. It was therefore important to adjust any bias in this sample which could have led to an overrepresentation of a particular breed or group of breeds. Given that the most critical longevity differences are between cows producing in dairy or beef herds, rather than between breeds in the beef herd, there was a need for adjustment between beef and dairy but not between individual beef breeds. This was achieved by a further search of BCMS/SAC, identifying the subset of records that included the dam. These records were scaled to the Defra slaughter totals, using BCMS/SAC to provide breed proportions, and to estimate the number of prime cattle originating from the national beef and dairy herds respectively. A conditional probability calculation, using animals registered as dead in 2008 at in BCMS/SAC, showed that dairy breed coded females of calving age were 1.29 times as likely to be dead within the lifespan of a the average prime animal as beef breed coded females of calving age (see Appendix 1). The proportion of prime cattle records with dairy dams were reduced accordingly.

2.2.3. Interpretation of breed coding in BCMS.

For the purposes of this study, it was assumed that an animal's breed code as it appeared in BCMS/SAC referred to the breed of its sire. The Cattle Book (Defra, 2007) for example describes the cattle breed field in BCMS as 'usually based on the breed of sire'. However this protocol was not explicitly stated in BCMS literature (Cattle Keepers Handbook, 2009). If the animals breed code contained an X (denoting a cross-bred) it was assumed that this referred to the animal itself being cross-bred, rather its sire. Therefore a LIMX coded animal was presumed to be the product of the mating between a pure-bred Limousin bull and any dam other than a pure-bred Limousin. Breed coding was inconsistent prior to 2000, and to a lesser extent post 2000, in BCMS. For example Limousin cattle appear to have been coded in 6 different ways (excluding crosses) up until 2000 (Lim, Lm, Li, L, LimB and

LimR). As such pure breed numbers in pre-2000 born animals in this study reflect the amalgamation of such codes for each breed. Since this was primarily a beef breed study, all Holstein or Friesian cattle (and variants such as British Friesian) were classed as Holstein/Friesian. It was also assumed that dairy sired females were not used as suckler cows in the beef breeding herd. Blonde d 'Aquitaine and Belgian Blue breed societies have now re-named themselves as British Blonde and British Blue respectively. For the purposes of this paper, the original names will be used since the majority of animals of these breeds in the dataset were born prior to these changes.

Breed codes were also not necessarily a good indicator of pure or cross-bred status. For instance, only 38% of animals coded AA (Angus pure breed code) in the data born since 2000 and dead by 2008, actually had dams coded AA, 11% were coded AAX (Angus cross- bred code) with 51% of dams having a variety of other (non-angus) breed codes. This was not an issue exclusive to AA, with for example, only 43% of animals coded CH having dams also coded CH, 8% were coded CHX with the rest again having a variety of other codes. This coding pattern confirms the assertion that animals are coded by sire breed rather than the breed makeup of the animal itself.

The approximate genetic makeup of animals was therefore calculated by using their sire and maternal grand sire (MGS) breed codes. These sires were assumed to be purebred, as per the literature (Penny *et al.* 2001; Todd, 2007). For example, an animal coded CH or CHX, with a dam coded LIM or LIMX was interpreted as being 50% Charolais and 25% Limousin, with the other 25% unknown. This remaining 25%, effectively the genetic makeup of the maternal grand dam (MGD), could not be calculated from BCMS/SAC due to very low numbers of animal records in BCMS/SAC with maternal great grandsire breed codes. In summary, BCMS/SAC provided an extensive profile of the sire and maternal grandsire breeds for the prime

slaughter and adult breeding populations, constituting 75% of the animal's genetic makeup. To overcome this problem, the remaining 25% was estimated according to Appendix 2, which calculated the overall proportion of beef and dairy genetics in the respective populations.

2.2.4. Suckler cows

In estimating the breed proportions of suckler cows, no correction was made for survival of dairy sired dams being less than beef sired dams. Although Appendix 1 did show that beef dams live longer than their dairy counterparts, the average lifespan of the progeny in this case (the suckler cow) was much older (98 months in 2007 BCMS/SAC) and the pattern of death suggested that it was not necessary to correct for dairy dam survival.

The most common suckler cow genotypes (in terms of the animal and its dam's breed codes) were estimated from females with a beef sire aged over thirty months at death in 2007 in BCMS/SAC. No edit was carried out regarding purebred (and potentially pedigree) females as these could not be reliably separated in the data set, but will make up less than 5% of cows defined in this way. Again similar breed codes were combined, including cross-bred codes (for example a LIMX x AAX was categorized with LIM x AA and referred to as a Limousin cross Angus). This search again yielded a reduced data sample in BCMS/SAC, with the same issue as in the prime slaughter animal study of the dam having to be recorded as dead in BCMS/SAC for the animal's record to appear. The assumption nevertheless was that this would still be a representative sample of suckler cows in 2007. These results were scaled to the beef breeding female population estimate from the 2006 Defra survey of 1.9 million head.

2.2.5. Artificial insemination and natural service

Estimating the numbers of AI sired animals in the beef and dairy herds was achieved using information from a commercial AI company (Genus PLC) and an UK Office of Fair Trading (OFT) report (Genus PLC, Crewe, UK, personal communication; OFT, 2004). OFT estimated that 3% of females in the beef herd were bred to AI. Given that the 2008 B x B prime slaughter population numbers 1.16 million (Table 2.1.), around 35,000 of these would therefore have been AI sired assuming that 1 calf is born from every 2.5 straws of semen sold (Genus PLC, Crewe, UK, personal communication).This would have required approximately 90,000 straws of beef semen, and from the total estimated annual beef semen market in the UK of 1.1 million straws, this would have left 1,010,000 straws for use in the dairy resulting in 404,000 beef AI sired calves in that sector.

NS breeding bull numbers and breed proportions were estimated from a combination of; the Defra slaughter census, Defra farm surveys, AI statistics and BCMS/SAC males aged over 47 months at death, with identical sire and MGS breed codes (eg.CH animal and CH dam or SM animal and SM dam). All cross-breds (23% of records) were removed from the data as it was considered that the proportion of cross-bred breeding males in the national cattle herd was less than 1% (Penny *et al.* 2001; Todd, 2007). The over 47 months criteria was used to estimate breed proportions, rather than over 30 months, because of the phenomenon of a small percentage of animals intended for beef (almost certainly male castrates) being culled aged over thirty months, probably in error rather than by design. Although these over 30 month culls represent a small proportion of prime culls, they are enough to confound the relatively small numbers of adult breeding bulls dying each year. To triangulate and provide additional information, these BCMS/SAC over 47 month breed proportions were also compared with BCMS annual registration data (published for the top 5 breeds by the British Limousin Cattle Society) and

estimates of AI sired calves from industry statistics (Genus, personal communication) to estimate total breeding bull numbers according to varying cow to bull mating ratios. Estimating numbers of breeding bulls aged under thirty one months at death was not feasible using BCMS/SAC, given that not all males with identical sire and MGS pure breed codes would necessarily have been destined for breeding purposes. As mentioned above, in order to estimate breeding bull numbers a survival probability was calculated from bulls aged over thirty months at death, from the top seven beef breeds with deaths recorded in 2008. This provided a lifespan pattern for breeding bulls with which to estimate the numbers of bulls alive in the population at any one time, and importantly the numbers entering service annually. The survival probabilities for breeding bulls aged between 18 and 42 months were obtained from McGowan (2006) and Todd (2007), since breeding bulls and male castrates in this age range could not be reliably separated in BCMS/SAC.

2.2.6. Pedigree

In order to establish whether potential breeding males within BCMS/SAC were pedigree, the BCMS records of Belgian Blue, Charolais and Limousin males were cross checked against information in the publically accessible genetic evaluation databases, BASCO and Breedplan. Estimates of pedigree cattle numbers were based on records of cattle born after 2000, because in 2000 all UK registration numbers were standardised and changed to a numeric format (BCMS, 2009). Cross referencing registration numbers of cattle born prior to 2000 was found to be unreliable due to differences in formatting between BCMS and BASCO/Breedplan records, as well as inconsistency in formatting within BCMS itself.

2.2.7. Relationship between sale prices and terminal selection index of breeding bulls.

As an indication of the use of selection indices by bull buyers, the sale price of pedigree bulls of the four top breeds numerically sold at official 2009/2010 breed sales was correlated with the Limousin Beef Value index (for Limousin) and the Terminal Sire Index for Angus, Charolais and Simmental.

2.3. Results and Discussion

2.3.1. Prime slaughter population.

In total 2,018,563 cattle aged under 31 months at death were recorded as having died in Great Britain in 2008 BCMS/SAC. Of these, 89% or 1.80 million of these animals died between 10 and 30 months of age, reflective of prime slaughter ages. This compares with 1.72 million animals in the collated Defra GB slaughter statistics for 2008, which is 4.3% lower and consistent with expected mortality levels in beef rearing systems (SAC, 2009), since slaughter statistics do not include on-farm deaths. Given that Defra slaughter statistics suggests 18% of total UK prime slaughter cattle are born in NI, scaling for this, the estimated UK prime slaughter population total would have been 2.12 million (2,018,563 x 0.89 x 1.18).

Table 2.1 shows a breakdown of this 2008 prime slaughter population by herd of origin. Here, beef x beef animals were born in the suckler herd, whilst beef x dairy and dairy x dairy were born in the dairy herd. Holstein/Friesian accounted for 95% of dairy breed codes in BCMS/SAC.

Table 2.1 The 2008 prime slaughter population, categorized by beef (B) or dairy (D) type.

	BxB ♂	BxD ♂	DxD ♂	BxB ♀	BxD ♀	DxD ♀	Total BxB	Total xD
GB proportions[a]	0.28	0.22	0.10	0.22	0.16	0.02		
UK proportions[b]	0.32	0.19	0.09	0.25	0.13	0.02	0.57	0.43
UK totals (000's)	647	378	183	513	272	36	1160	869

[a]Unadjusted 2008 BCMS/SAC data
[b]2008 BCMS/SAC data adjusted for Northern Ireland and dairy dams
BxB ♂ represent males with a beef breed sire and a beef breed maternal grand sire.
DxD ♀ represent females with a dairy sire and a dairy maternal grand sire.
Prime animals were defined as those aged between 10 and 30 months inclusive at death.

From this information the proportions of genetics coming from NS beef bulls, AI beef bulls and dairy bulls in the prime beef population was estimated using Appendix 2. Assuming equal use of NS and AI sired beef x dairy females replacement females, the relative genetic proportions were estimated as: 47.8% NS beef, 16.6% AI beef and 35.6% dairy. Therefore the prime slaughter population was composed of 64% beef and 36% dairy genetics. It should be noted that the proportion of dairy genetics in this population is heavily reliant on the numbers of dairy sired bull calves actually reared to prime slaughter, given the high rates of slaughter of these calves at birth. Typically only 50% of dairy sired calves have been reared beyond birth in the last 5 years (Beyond calf exports stakeholders, 2010).

2.3.2. Prime breed composition.

Recently imported European breeds contribute the majority (around 50.5%) of all the genetics in this prime slaughter population, with ‘native’ British breeds contributing less than 14% (Table 2.2.). Limousin is the most influential beef breed in the UK with just over a fifth of the genetic contribution to the prime slaughter population. The top seven beef breeds include two British breeds and combined account for 61% of the

total genetics and 94% of the beef contribution. These are the only breeds which are used on a nationwide basis in the UK, and are also those beef breeds with significant sales for UK AI companies (Genus 2010, personal communication).

The relative use of the most popular beef sire breeds in the beef and dairy sectors is shown in Table 2.3., with Limousin, Belgian Blue and Angus being equally popular across beef and dairy herds. Charolais, by contrast, is much more heavily used in the beef herd.

Table 2.2 Breed genetic contribution to the 2008 prime slaughter population

Breed	Breed code	[a]Sire	[a]MGS	[b]Remainder	Total
Limousin	LIM	15.5	4.6	1.7	21.8
Charolais	CH	9.3	1.3	0.5	11.1
Simmental	SM	5.2	2.6	1.0	8.8
Belgian Blue	BB	4.5	1.0	0.4	5.9
Blonde	BA	1.8	0.4	0.1	2.3
Other imported beef		0.4	0.2	<0.1	0.6
Total imported beef					50.5
Holstein/Friesian	HF	4.5	9.7	18.4	32.6
Native dairy		0.1	0.3	1.2	1.6
Other imported dairy		0.3	0.3	1.2	1.8
Total Dairy					36.0
Aberdeen Angus	AA	4.4	1.9	0.7	7.0
Hereford	HE	1.9	1.3	0.5	3.7
South Devon	SD	0.6	0.3	0.1	1.0
Welsh Black	WB	0.3	0.2	0.1	0.6
Devon	DEV	0.2	0.1	<0.1	0.3
Galloway	GA	0.1	0.1	<0.1	0.2
Highland	HI	0.1	0.1	<0.1	0.2
Other native beef		0.3	0.2	<0.1	0.5
Total native beef					13.5
Total		50	25	25	100

[a] Figures calculated from BCMS/SAC. Contributions were adjusted according to beef or dairy dam survival probability.

[b] Estimated remaining 25% of genes, made up of the MGD. This could not be calculated from BCMS/SAC. The Holstein/Friesian proportion was therefore estimated according to appendix 2, which calculated that 36% of the genes in this population were from dairy breeds, and that Holstein-Friesian makes up 95% of the dairy contribution. The remaining MGD contribution was then assigned pro rata to the beef breeds as per their MGS proportions.

Table 2.3 A comparison of the beef breed sire use (natural service plus artificial insemination) in beef and dairy herds (estimated from 2008 prime slaughter population).

Breed	% beef herd	% dairy herd
Limousin	35	31
Charolais	20	8
Simmental	12	20
Belgian Blue	10	11
Angus	11	14
Others	12	16
Total	100	100

The differences between breed contributions in GB and NI are shown in Table 2.4., with notably greater use of Charolais in this latter region. However, as shown in Table 2.4., combining NI with the GB dataset only increases the overall sire contribution of Charolais by 2% whilst increasing Simmental and reducing Belgian Blue by 1% each. Therefore, in terms of breed use, BCMS was reasonably representative of the UK as a whole, and introduced only a small bias. The BCMS annual registration data shown in Table 2.4. can also be used to assess trends in breed use. Sensitivity over years was tested by extracting 2005, 2006, and 2007 BCMS/SAC data, with no major differences found in breed proportions. Similarly, 2008 BCMS birth registration data suggests only minor changes from 2005, with Limousin, Simmental and Belgian Blue identical and with Charolais 16% (down 2%) and Angus 13% (up 2%), (BLCS 2006; BLCS 2009).

Table 2.4 Births registered by beef sire breed in 2005 in BCMS (Great Britain) and APHIS (Northern Ireland) reproduced the 2006 BLCS studbook and factfinder (BLCS, 2006) ('000's,)

Sire Breed	BCMS	%	[a]APHIS	%	Total	%
Limousin	709	35	134	34	843	35
Charolais	358	18	115	29	473	20
Simmental	232	11	20	5	252	10
Angus	216	11	42	11	258	11
Belgian Blue	194	10	33	8	227	9
Others	308	15	55	14	363	15
Total	2017	100	399	100	2416	100

[a]APHIS is the Northern Ireland equivalent of the Cattle Tracing Scheme.

In the last 40 years, breed use in the UK beef herd has therefore changed dramatically, to the extent that around 75% of beef genes in the prime slaughter population are non-native. The Aberdeen Angus is the one native breed to have maintained a significant market share of beef genetics, in comparison with 1970's bull license data (Craven and Kilkenny, 1976), yet even the influence of this breed has halved within the above timescale.

2.3.3.

Suckler female population. Overall estimates of the total UK female breeding herd in 2006 were provided by Defra census information. These suggested that there were 1.9 million beef females (cows plus in calf heifers) and 2.4 million dairy females (cows plus in calf heifers). The estimated numbers of B x B males and females slaughtered (Table 2.1.) indicated that approximately 134,000 (647,000 - 513,000) females were retained within the suckler herd for breeding in 2008. Similarly, the numbers of B x D males and females suggested that 106,000 beef sired females from the dairy herd were kept as replacement suckler cows in 2008. Therefore 44% of replacement suckler breeding females came from the dairy herd in 2008.

2.3.4.

Breed composition of suckler females. Females retained within the suckler herd per breed of sire are shown in Table 2.5., with 94% of these sired by the top seven breeds identified previously. In 2008, 23% (204k / 829k x 100) of females sired by a beef bull were retained as suckler cows. Only 11.5% of prime matings therefore resulted in a female kept for breeding.

Table 2.5 Estimated numbers of females retained for suckler breeding, by sire breed from the 2008 prime slaughter population in BCMS/SAC, percentages retained of each sire breed and of total females.

Sire Breed	Males	Females	[a] Retained	% of sire breed retained	% of total females retained
Limousin	305151	242532	62619	21	31
Angus	101405	66561	34844	34	17
Simmental	98720	66699	32021	32	16
Belgian Blue	82770	57536	25234	30	12
Hereford	42908	26203	16705	39	8
Charolais	152134	135783	16351	11	8
Blonde	34006	29979	4027	12	2
Others	52155	39912	12243	-	6
Total	869249	665205	204044	-	100

[a] Retained = Males minus Females and assumes a 50:50 ratio of males to females reared to slaughter age.

If 44% of these 'replacement' matings occur in the dairy herd (as described above), then only 7% of matings in the suckler herd are intended to be kept as breeding females. This implies that 93% of matings in the UK suckler herd are arranged with a terminal goal in mind. The breed contributions to replacement suckler females (Table 2.6.) show a similar pattern to the prime slaughter animals, with slightly more Angus and Hereford influence. Commonly regarded as the most extreme terminal beef breed, the Belgian Blue actually has similar contributions to both prime slaughter and replacements. In contrast, the Charolais influence is halved in the suckler female group. This is reflective of the high use of Belgian Blue AI in the dairy herd, and consequent availability of Belgian Blue X dairy females, as well as the

positive contribution to suckler carcass traits of the Belgian Blue. Indeed these two breeds were at opposite extremes in terms of their pattern of use, with Belgian Blue being largely an AI breed with relatively low levels of NS, whilst Charolais is largely a NS breed with low AI use.

Table 2.6 Breed genetic contributions to the 2007 suckler female population.

Breed	Sire[b]	MGS[b]	[c]Remainder	Total %
Limousin	14.2	3.0	0.8	18.0
Charolais	4.5	1.4	0.3	6.2
Simmental	7.1	3.4	0.9	11.4
Angus	6.3	1.6	0.4	8.3
Belgian Blue	4.7	0.7	0.2	5.5
Hereford	3.7	1.1	0.3	5.2
Blonde	1.4	0.3	0.1	1.9
Holstein/Friesian[a]	-	10.3	18.0	28.2
Others	8.0	3.3	4.2	15.5
Total	50	25	25	100.0

[a] It was assumed that no Holstein/Friesian sired (or other dairy breed) females were used as suckler cows.
[b]Figures calculated from beef sired females aged >30 months at death in 2007 BCMS/SAC.
[c]Estimated remaining 25% of genes, made up of the MGD's which could not be calculated from BCMS/SAC. The Holstein/Friesian proportion was therefore estimated according to appendix 2, which calculated that 29.7% of the genes in this population were from dairy breeds, and that Holstein-Friesian makes up 95% of the dairy contribution. The remaining MGD contribution was then assigned pro rata to the beef breeds as per their MGS proportions.

The 10.3% Holstein/Friesian MGS contribution to suckler females is consistent (10.3 /25 /0.95 = 43.4%) with approximately 44% of suckler cows being born in the dairy herd in Table 2.1. All together, 94.3% of these 2007 suckler females were cross-bred (as defined by those without two matching sire and grand sire pure breed codes).

The most popular suckler cow genotypes are shown in Table 2.7, with a very diverse range of breed combinations present. Interestingly the two most popular genotype groupings appear to be either first generation crosses from the dairy herd or 'three-quarter' bred suckler beef replacements (with the same breed of sire and

MGS). Although this Table only includes 54% of sucklers, if there was wide-scale rotational cross-breeding in UK suckler herds, it would be expected to feature among the most popular genotypes. However, the most common rotational breed mix, Limousin x Simmental (which was the most common female with different beef breed sire and MGS) breed only accounts for 2.9% of total sucklers.

Table 2.7 The 10 most common suckler cow genotypes in the United Kingdom estimated from 2007 BCMS/SAC.

Sire	MGS	%	number of females ('000's)
Limousin	Holstein/Friesian	10.7	203
Limousin	Limousin	8.1	153
Simmental	Simmental	6.0	114
Belgian Blue	Holstein/Friesian	5.9	111
Hereford	Holstein/Friesian	5.3	101
Angus	Holstein/Friesian	4.5	85
Simmental	Holstein/Friesian	4.4	84
Angus	Angus	3.6	68
Charolais	Charolais	3.4	65
Limousin	Simmental	2.9	55
Total (top 10)		54.8	1039

2.3.5 Breeding Bulls.

The assumption that very few cross-bred breeding bulls were in use and that cross-bred males aged over thirty months at death were actually castrates is supported by Figure 2.2 which show a 'spill over' from the huge drop off in male slaughtering around the 30 month age limit. A more detailed view of male deaths, for animals with identical beef sire and MGD breed codes, in Figure 2.3 shows a dip in deaths around 47 months before resuming a temporary upward trend, which is consistent with the hypothesis that this profile is a mix of the distributions of slaughter and breeding males.

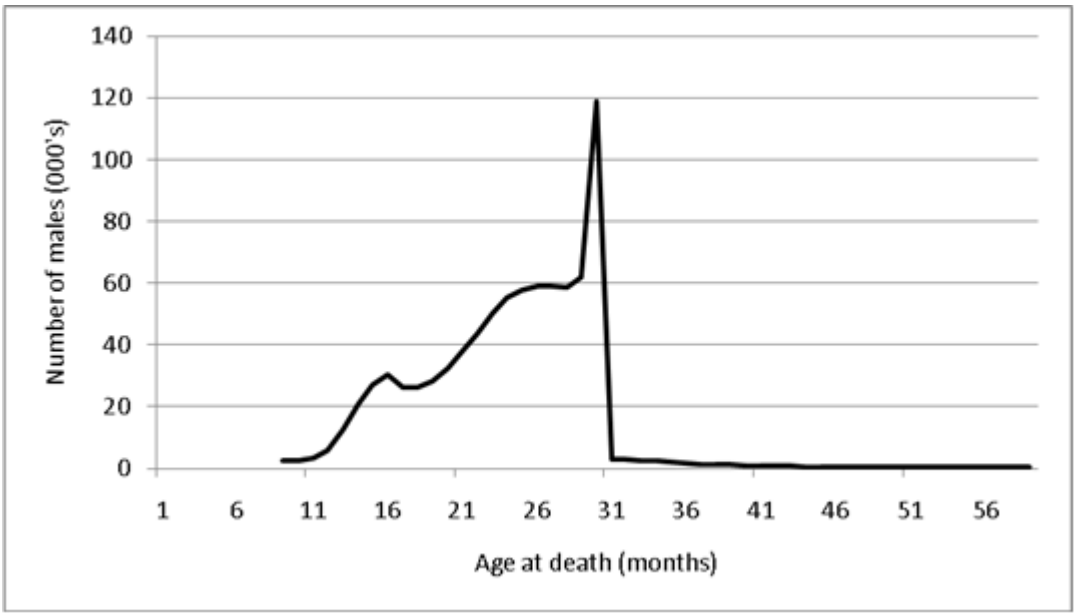

Figure 2.2 The pattern of male deaths for beef sired males aged between 8 and 58 months at death inclusive in 2008.

The 2004 Defra census reported 101,000 total breeding bulls in the UK (the last year for which this total is available) (Defra, 2004). From dairy AI statistics (Genus PLC, personal communication), it was estimated that there were around 200,000 NS dairy calves in 2005. Assuming a conservative mating ratio of 20 calves per bull would suggest that around 10,000 NS dairy bulls were included in the Defra census total. Thus, the estimated NS beef bull population in 2006 was 91,000, and this figure was used in Tables 2.8 and 2.9 to further estimate numbers of bulls by breed. Table 2.8 shows the estimated numbers of NS bulls required to sire the approximate number of NS bred calves born in 2005. Three different calves/bull ratios are shown, depicting likely breeding ratios.

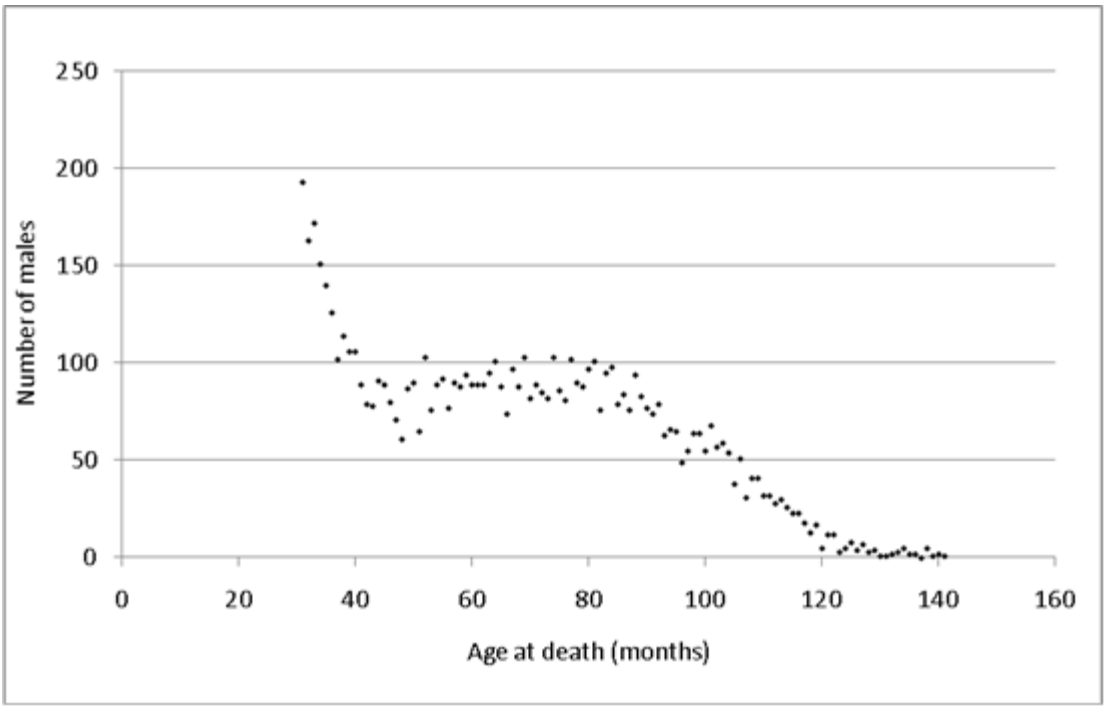

Figure 2.3 The age at death profile of males aged over 30 months of age at death in 2008 with pure bred sire and MGS from the top seven beef breeds.

Table 2.8 Numbers of beef sired calves born in 2006 by artificial insemination (AI) and natural service (NS), and NS sires required to father them and estimated number of bulls in BCMS/SAC aged over 47 months at death ('000's).

Breed of sire	UK calves registered in 2005			Numbers of NS sires required			[a]BCMS/ SAC <47 month bulls
	Total	AI sired	NS sired	@ 20 calves/sire	@ 25 calves/sire	@30 calves/sire	
Limousin	843	150	697	34.9	27.9	23.2	26.4
Charolais	473	16	457	22.9	18.3	15.2	18.2
Simmental	252	17	235	11.8	9.4	7.8	10.9
Angus	258	40	218	10.9	8.7	7.3	11.8
Belgian Blue	227	170	57	2.9	2.3	1.9	3.6
Others	363	11	348	17.4	13.9	11.6	20.0
Total	2416	404	2012	100.8	80.5	67.0	91.0

[a]This column gives an estimate of the numbers of the NS beef bulls present in 2006 by breed in the national cattle herd from an estimated total of 91,000 bulls in use, using breed proportions from males aged over 47 months at death in 2005 BCMS/SAC.

Table 2.9 uses a survival pattern from beef bulls aged over thirty months at death, from the top seven breeds with two identical sire and MGS pure breed codes recorded in BCMS/SAC as having died in 2008.

Table 2.9 The age profile of natural service beef breeding bulls in use in the national herd in 2006.

[a]Bull age (months)	[c]Survival probability	Total[d]	Limousin	Charolais	Belgian Blue
18[b]	0.90	20115	5836	4023	796
30[b]	0.89	18065	5241	3613	715
42	0.82	16014	4646	3203	634
54	0.77	13184	3825	2637	522
66	0.70	10109	2933	2022	400
78	0.57	7033	2041	1407	278
90	0.46	4019	1166	804	159
102	0.28	1845	535	369	73
114	0.20	513	149	103	20
126	0.01	104	30	21	4
Total		91000	26402	18200	3601

[a] Bulls were assumed to enter breeding service in herds at an average age of 18 months
[b] Numbers in years one and two have been adjusted to remove castrates according to literature estimates of breeding bull deaths in these years (McGowan, 2006; Todd, 2007).
[c] Survival probability derived from 2008 BCMS/SAC data for bulls aged <30 months at death, and refers to the probability of a bull surviving the following 12 months.
[d] It was assumed that 91,000 bulls were in service in 2006.

The estimated average herd life of these bulls was 4.5 years with only minor between breed differences. Therefore, assuming a total of 91,000 NS beef breeding bulls total translates to approximately 20,000 breeding bulls entering service each year. This is similar to the study of Amer (2007) which estimated 19,346 beef sires purchased by commercial farmers each year. Further support for these estimates comes from Defra slaughter statistics which recorded 17,800 adult bull culls in 2008 and 19,600 in 2009 (Defra, 2010). Survival probabilities for 10 years of service are shown, as well as calculations for three individual breeds. Estimates of breeding bulls entering service each year (row 1), are in reasonable agreement with approximate annual pedigree registrations for 2008. For example, there were approximately 4000 Charolais males registered in 2008 (BCCS, 2009) and

approximately 900 Belgian Blue (BBCS, 2009). Limousin registrations were somewhat higher than the figure in Table 2.9 at approximately 8000 (BLCS, 2009). The pedigree registration of a bull is not a guarantee it will become a breeding animal. It is also likely that Limousins are popular with breeders maintaining closed beef production systems. Therefore in the same way that large numbers of Holstein dairy cows are pedigreed without necessarily being elite breeding animals, a similar system may be employed in some Limousin herds.

2.3.6. Sire Identification

The proportion of prime animals with UK registration number sire identifications (id) included in their BCMS records varied from just 9% of Belgian Blue sired animals up to 37% of Angus sired animals, among the top 7 beef breeds. The other five of the top seven beef breeds were all in the range between 21% and 28%. Approximately 1% of animals had other sire id variants such as breed, name of sire or tattoo numbers. No individual sire had more than 100 progeny in this data set, suggesting an absence of AI sire recording. As such BCMS does not provide an unbiased sample of sire identification numbers. The lack of AI sire recording also explains the particularly low figure for Belgian Blue sire id, given that the vast majority of calves from this breed are AI bred (Table 2.8).

2.3.7. Influence of pedigree breeding

The extent to which the historical practice of registering pure-bred breeding males in pedigree herdbooks still exists was of major interest in characterising the UK breeding industry. This analysis again focused on males aged over 47 months at death as these were seen as the group which could most reliably be interpreted as breeding males. Sampling the first 100 Charolais males by date of birth (with CH Sire and MGS breed codes), born in 2000 and aged over 47 months at death in

BCMS/SAC, 84% were registered as pedigree males in the ABRI database. Similarly, 90% of the first 100 Belgian Blue coded BB (sire and MGS) males born in 2000 and aged over 47 months at death were recorded in the ABRI database as pedigree. Limousin numbers were slightly lower, with 76% of the first 100 Limousin coded LM (sire and MGS) males born in 2000 and aged over 47 months at death were recorded in the BASCO database as pedigree. These figures constitute a lower estimate given the formatting differences between BCMS and the pedigree databases. Cross referencing BCMS/SAC with ABRI and BASCO therefore suggested that the majority of animals which could be reasonably expected to be breeding bulls (i.e. aged over 47months at death) were pedigree. It did appear however that there may be significant numbers of non registered purebred bulls in use, perhaps as high as 24% in Limousin.

Investigation of males aged just over 30 months of age at death highlighted the problem of males reared for slaughter confounding the identification in BCMS/SAC of breeding males culled early in their reproductive careers. Taking all of the 2002 born Belgian Blue (coded BB) (39) and CH (75) males in BCMS/SAC age 31 to 33 months at death, 49% of BB and 47% of CH were registered in the ABRI database as being pedigree, or had an imported identification number (suggesting imported breeding bulls). This adds further evidence to the suggestion that males culled at just over 30 months of age are a mixture of beef steers and breeding bulls (see also Figure 2.3).

2.3.8. Relationship between sale prices and terminal selection indices of breeding bulls.

Correlations between sale prices of breeding bulls and terminal selection indices were significant ($P<0.01$), but of a moderate strength (Table 2.10). Terminal index ranges in this Table are presented in the standard industry format, although there are minor differences between the trait composition of the Signet Limousin Beef Value index and the ABRI Terminal indices of the other three breeds. The regressions suggest that there is greater value attached to bulls with higher index values. This analysis would suggest that genetic breeding values and recorded weights do play a part in purchasing decisions, although phenotypic selection remains a key element in bull buying strategy in practise. Unlike the dairy sector, there are no formal structural soundness evaluations of pedigree beef cattle in the UK. It is therefore left up to the judgement of the purchaser as to whether an animal is sufficiently sound to carry out its breeding roles, and deliver its genetic merit effectively.

Table 2.10 Relationship between sale price and terminal index of young breeding bulls sold at official breed society sales in 2009/10.

[1]Terminal index range	Limousin	£	Charolais	£	Angus	£	Simmental	£
	Number sold	Mean price	Number sold	Mean price	Number sold	Mean price	Number sold	Mean price
Top 1%	84	7495	31	6740	23	8845	6	6843
2-10%	235	6549	85	6769	79	4564	26	4862
11-25%	155	5252	67	6048	33	3400	27	3999
26-50%	110	4654	79	5279	9	3540	15	3724
Below median	51	3717	83	4131	5	3633	8	3545
Total bulls sold	635		345		149		82	
Correlation	0.25		0.21		0.38		0.32	
Regression (£/index point)	160		112		255		181	

[1]Terminal index refers to Limousin Beef Value and Charolais, Angus and Simmental terminal selection indices.

2.3.9. Utility of BCMS as a data source.

The BCMS database provided valuable information regarding breed use in the national beef herd. Records of dead animals were particularly useful in investigating the prime slaughter population, and it was possible to make estimates of breeding animal numbers which triangulated reasonably well with other information sources. Greater recording of sire identification numbers by BCMS users would considerably enhance the commercial and research potential of this information source. Additionally, tighter adherence to breed coding protocol would greatly improve the data quality, removing the need for user interpretation of actual breed. This issue can be overcome, at a cost of effort and accuracy, by taking into account the breed codes in the animals' ancestry. In doing this, it is possible to interpret the data, and produce a more valid estimate of breed proportions and genetic influence. However, BCMS has the potential to become the database of choice for monitoring of UK cattle genetic resources with only minor adjustments to animal recording protocol.

2.4. Conclusion

This study has provided detailed population-wide evidence of the breed composition of UK beef cattle. Cross-breeding has been shown to be the overwhelming approach in suckler herds, in sharp contrast to dominance of pure-bred pedigree breeding in the selection of NS sires. Evidence was obtained which showed EBV technology to be a moderately important criterion in the purchase of these sires. Importantly, it was established that Holstein-Friesian genes continue to play a large role in the beef herd. In particular 40% of replacement suckler cows are by-products of the dairy herd. Combining this gene-flow with the pronounced longevity of suckler cows, dictates that there are very few intended maternal matings. Consequently nine out of ten matings in the suckler herd result in progeny being slaughtered at a prime age.

2.5. Appendices

2.5.1. Appendix 1; Predicting the survival of beef and dairy sired dams.

The objective is to calculate the probability that a randomly chosen calf has a dam which dies in the next two years. This calculation uses females recorded in BCMS/SAC as dying in 2008 and estimates the probability that a female will die within the average lifespan (24 months) of her prime slaughter progeny. It is assumed that a typical dairy-sired female first calves at 24 months of age and that the average beef-sired female at 30 months of age, and that there is a stable age distribution.

Example calculation from Table 2.11. The total dying from 24 to 179 months of age (2,363,000), equates to an estimate of the size of the breeding population, which is similar to the national dairy breeding female herd estimate (Defra, 2008b). All these will be assumed to first breed in the period 24-35 months of age, therefore the number of breeding females in row 1 is equivalent to the annual replacement rate. Of these replacements, 32,000 die before the end of the age period, leaving 414,000 females to enter the next age. Therefore, the fraction of calves born in a population from 36 to 47 month old females, P1, is 414/2363 = 0.175. For a calf born to a 36 to 47 month old female, the probability its dam dying in the next two periods, Q1, is (46 +57)/414 = 0.249.

Therefore the sum of the product of (P1 x Q1) across all age periods is the probability that among calves born to dairy-sired cows, a dam of a randomly chosen calf dies in the next two years (0.466). The calculation in Table 2.12 follows a similar pattern to arrive at a probability among calves born to beef-sired cows, the probability that the dam of a randomly chosen calf dies in the next 2 years is 0.362.

Therefore, the dairy-sired dams were 1.29 (0.466/0.362) times as likely die in the lifetime of their prime slaughter progeny as beef-sired dams.

Table 2.11 Probability of a dairy-sired dam dying within the lifespan of her prime slaughter progeny, using dairy-sired females recorded as dying in 2008 in BCMS/SAC. A full description of this calculation is described in the text.

Age group (months)	Number dying within age group ('000's)	Number alive at the start of age group ('000's)	Fraction of total calves assumed born to females in age group (P1)	Fraction of females not surviving two consecutive age groups (Q1)	Probability that a dam of randomly chosen calf dies in the next two years (P1 x Q1)
24-35	32	446	0.189	0.175	0.033
36-47	46	414	0.175	0.249	0.044
48-59	57	368	0.156	0.321	0.050
60-71	61	311	0.132	0.373	0.049
72-83	55	250	0.106	0.420	0.044
84-95	50	195	0.083	0.492	0.041
96-107	46	145	0.061	0.545	0.033
108-119	33	99	0.042	0.616	0.026
120-131	28	66	0.028	0.697	0.019
132-143	18	38	0.016	0.763	0.012
144-155	11	20	0.008	0.900	0.008
156-167	7	9	0.004	1.000	0.004
168-179	2	2	0.001	1.000	0.001
Total	446	2363	1.000	8.746	0.466

Table 2.12 Probability of a beef-sired dam dying within the lifespan of her prime slaughter progeny, using beef-sired females recorded as dying in 2008 in BCMS/SAC. A full description of this calculation is described in the text.

Age group (months)	Number dying within age group ('000's)	Number alive at the start of age group ('000's)	Fraction of total calves assumed born to females in age group (P1)	Fraction of females not surviving two consecutive age groups (Q1)	Probability that a dam of randomly chosen calf dies in the next two years (P1 x Q1)
30-41	34	246	0.156	0.240	0.037
42-53	25	212	0.135	0.212	0.029
54-65	20	187	0.119	0.214	0.025
66-77	20	167	0.106	0.234	0.025
78-89	19	147	0.093	0.265	0.025
90-101	20	128	0.081	0.297	0.024
102-113	18	108	0.069	0.269	0.018
114-125	11	90	0.057	0.244	0.014
126-137	11	79	0.050	0.291	0.015
138-149	12	68	0.043	0.471	0.020
150-161	20	56	0.036	0.625	0.022
162-173	15	36	0.023	0.639	0.015
174-185	8	21	0.013	0.619	0.008
186-197	5	13	0.008	0.692	0.006
198-209	4	8	0.005	0.625	0.003
210-221	1	4	0.003	0.750	0.002
222-233	2	3	0.002	1.000	0.002
234-245	1	1	0.001	1.000	0.001
Total	246	1574	1.000	10.283	0.362

2.6.2. Appendix 2; **Genetic composition of the prime beef population.**

The breeding notation used in the following refers to the origin of the sire and the maternal grand-sire (MGS), so that B x D is an animal with a beef sire and a dairy MGS. The prime slaughter population comprises offspring from B x B, B x D and D x D breeding females sired by beef and dairy bulls. It is assumed that dairy bulls are only used on D x D females. The term suckler herd refers to all the B x B and B x D females. Whilst BCMS/SAC provided breed information on the sire and maternal grand sire (MGS), the remaining 25% of the breed composition determined by the maternal grand dam (MGD) was required to be estimated. This was done using the gene flow diagram shown in Figure 2.1 and explained below. The fraction of the genome deriving from beef bulls by natural service (NS) and artificial insemination (AI) was also considered as this is related to the intensity of selection that is being practiced in the beef herd. This fraction was defined by tracing back the pedigree to male ancestors, so that a NS beef sire contributes 0.5 to the NS beef fraction, a NS beef MGS contributes 0.25 to the NS beef fraction, a NS beef sire to the maternal grand-dam contributes 0.125 to the NS beef fraction and so on.

The calculation requires the following parameters that were obtained from BCMS/SAC, OFT (2004) and Genus plc (personal communication): S_B = proportion of beef-sired calves from NS within the suckler herd = 0.97; S_D = proportion of beef-sired calves from NS within the dairy herd = 0.38; P_{BB} = proportion of breeding females in suckler herd that is B x B = 0.56; P_{BD} = proportion of breeding females in suckler herd that is B x D = 1 - P_{BB} = 0.44; Q_{BB} = proportion of prime slaughter population that are B x B = 0.57; Q_{BD} = proportion of prime slaughter population that are B x D = 0.32; Q_{DD} = proportion of prime slaughter population that are D x D = 1 – Q_{BB} – Q_{BD} = 0.11. This is summarised by the gene flow in Fig. 1.

Then the gene flow of beef genes via NS in the B x B female (P_1) is calculated by considering such a female as an offspring of a B x (B x B) mating and then as an offspring of a B x (B x D) mating to give:

$P_1 = P_{BB} (0.5 S_B + 0.5 P_1) + P_{BD} (0.5 S_B + 0.25 S_D)$

Solving for P_1 gives $P_1 = 0.7316$.

Similarly, the gene flow of beef genes via AI in the B x B female (P_2) is:

$P_2 = P_{BB} (0.5 (1 – S_B) + 0.5 P_2) + P_{BD} (0.5 (1 – S_B) + 0.25(1-S_D)) = 0.1155$

Solving for P_2 gives $P_2 = 0.1155$.

The remaining fraction is 1 – 0.7316 – 0.1155 = 0.1529 and is gene flow from dairy breeds.

The gene flow of beef genes via NS to the prime slaughter population is then given by

$$0.5 Q_{BB} S_B + 0.5 Q_{BD} S_D + 0.5 Q_{BB} P_{BB} P_1 + 0.5 Q_{BB} P_{BD} (0.5 S_D)$$

where the first two terms concern the flow of beef NS genes via the sires and the second two terms concern the flow from the dams. Note that prime slaughter animals that are B x D only have gene flow via NS of beef sires from their sire only, where as D x D animals have no gene flow from beef sires. Substituting the values gives 0.4776.

Similarly the gene flow of beef genes via AI is given by

$$0.5 Q_{BB} (1 - S_B) + 0.5 Q_{BD} (1 - S_D) + 0.5 Q_{BB} P_{BB} P_2 + 0.5 Q_{BB} P_{BD} 0.5 (1 - S_D)$$

and substituting values shows this to be 0.1658. Consequently in total beef breeds contribute 0.643 and dairy breeds 0.357 of the genes in the prime slaughter population.

The dairy MGD fraction is obtained by subtracting the fractions accounted for by dairy sires and dairy MGS. Dairy sires account for 0.5 Q_{DD} = 0.055 and dairy MGS account for 0.25 (Q_{BD} + Q_{DD}) = 0.108, leaving 0.194 of gene flow from dairy through MGD. Of this gene flow a fraction 0.95 will be from Holstein/Friesian (the proportion of dairy breed codes which are Holstein/Friesian in BCMS/SAC), i.e. a total gene flow of 0.184 from this breed to the prime slaughter population through MGD. The remaining dairy contribution of 0.010 through MGD will be from other dairy breeds and in Table 2.2 is included in 'Other' breeds, whilst the remaining contribution through MGD of 0.25 – 0.194 =0.056 was then assigned pro rata to the beef breeds according to their MGS proportions.

Chapter 3:

The breeding structure of the UK national pedigree Limousin herd

3.1. Introduction

Following the success of the Charolais importations in the 1960's, UK beef breeders were keen to experiment with other lean and fast growing European breeds (Limousin and Simmental Tests Steering Committee, 1976). The Limousin, along with the Simmental, was part of the second major wave of European beef breeds to arrive on UK shores in the later part of the 20th Century. The first shipment of 200 head of French Limousin cattle imported into the UK arrived at Leith Docks in Edinburgh in December 1970 (Jobst, 1986). A UK herdbook was established to pedigree register these founding animals. Initially through artificial insemination (AI) use in the dairy herd and later as natural service (NS) beef sires, the adoption of Limousin genetics was swift, and further importations of breeding animals followed annually (which continue to this day, albeit on a less regulated basis). From that modest numerical beginning in 1970 the Limousin breed grew to become the UK's most influential beef breed by the end of the 20th century. In Chapter 2, it was shown that Limousin genes were the most common among UK beef breeds, in all categories of beef breeding and slaughter cattle.

As well as all AI bulls being pedigree, Chapter 2 demonstrated that the majority (>75%) of NS Limousin breeding bulls used in the suckler herd were also pedigree registered. Given the influence of pedigree animals in beef breeding, it is important to understand the breeding structure of beef herdbooks and the effect this could have on the potential implementation of Genomic Selection (GS) in the UK. In this context it is also particularly relevant to investigate the influence of improved genetics within pedigree beef herdbooks.

Previous studies, across a variety of breeds, have suggested that an 'elite' core of bull breeding herds is responsible for the majority of gene flow within pedigree

populations. Robertson and Aker (1951) studied the British Friesian, Wiener (1952) the UK Ayrshire population, Ozkutuk and Bichard (1977) the UK Hereford, whilst two recent papers investigated the American Red Angus Marquez herdbook [Marquez and Garrick (2007); Marquez *et al.* (2009)].

The concept of the herd as the key level at which selection decisions are made, particularly in terms of social attitudes to genetic technology by breeders, is therefore an important one in beef cattle breeding, particularly considering the heavy reliance placed on the use of NS.

Some evidence of the uptake of EBV technology was shown in Chapter 2, where it was found that a moderate (but statistically significant) correlation exists between the sale price of young breeding bulls and their terminal selection index (TI). Furthermore, the genetic trend for TI in the Limousin breed is positive, although modest, at around a £1 per animal per year improvement (BASCO, 2011). Although these findings suggest a reasonable use of EBV technology among Limousin breeders, they do not necessarily imply that a classical pyramid system of selection is in place such as described by e.g. Simm (1998). This classical pyramid has an 'elite' group of herds driving selection and a multiplier group of pure-bred herds breeding NS males for use in commercial herds. The presence of such an elite group of herds within the breeding structure, actively using EBV technology, would be more favourable for GS implementation than a structure where those breeders utilising EBV were not influential across the breed. Furthermore, characterising the structure of the beef breeding pyramid will provide an insight into the rate of dissemination of improved genes to the commercial population.

Therefore, the aim of this study was to examine the UK Limousin pedigree herdbook, as an example population, with which to characterise herd structure and

evaluate the dissemination of improved genetics within the breeding core of the UK beef population. This study was also intended to provide key population parameters, including selection intensity and generation interval, for use in GS modelling in chapter 4. The continuing influence of imported genes within the herdbook will also be quantified.

3.2. Materials and Method

3.2.1. Data.

Pedigree, performance and genetic evaluation records held within the BASCO database were analysed to produce a profile of UK Limousin herds. Information entered in this database is subject to the national quality control. Records of cross-bred animals, which are included in UK Limousin breed genetic evaluations, were removed prior to analysis. Therefore, only Pedigree Limousin animals were included in the study.

Date of birth, herd of birth, calving ease, 400 day weight, TI, TI accuracy and imported status, were extracted in January 2011, for each animal born in 2009, and for each of their sires, dams and paternal grandsires (PGS). PGS was used as a classifier of herd influence, rather than all grandsires [i.e. PGS plus maternal grandsires [(MGS)], as selection intensity in beef breeds has been demonstrated to be twice as great for this former group (Marquez and Garrick, 2007). The selection intensity analysis in the current study also used data from 2003 and 2010.

3.2.2. 2009 Male cohort

The annual male registration cohort (MC) of pedigree bulls was used as the base group with which to define herd influence, selection intensity and generation interval. Chapter 2 demonstrated that NS bulls are the main disseminators of Limousin genes in the commercial suckler herd, and that these are largely selected from this pedigree cohort. There were 8270 males in the 2009 MC, born in 1279 herds (out of 1638 herds in total registering any pedigree calves in 2009), and sired by 1537 bulls with 728 PGS (see Tables 1 and 2).

3.2.3. Animals born outside the UK

Identification of animals born outside the UK, and their herd of birth categorisation, was complex. Their imported status and herd of birth is categorised according to three rules BASCO;

1) Imported live animals are assigned herd of birth identifiers (which therefore relate to non-UK herds) in BASCO and the animals are tagged as being 'imported'. Where herd of birth information was incomplete, animals are assigned the 'unknown' herd of birth identifier (999999).

2) Sires and PGS born outside the UK, whose semen was imported, are classified under a single herd grouping (14299) in BASCO. 1% of sires (which sired 2% of the 2009 MC) and 5% of PGS (which were the PGS of 9% of the 2009 MC) were categorised in this quasi herd of birth category. If these sires and PGS were subsequently also imported (i.e. the animal itself was imported as well as its semen), they were tagged with an imported flag, but remained in the 14299 category. This applied to 1 sire and 11 PGS (**<**2%).

3) Sires and PGS of imported animals, which were not themselves imported, or had their semen imported, or were born in the same (recognisable) herd as another

imported animal, are assigned the 'unknown' herd of birth identifier (999999) in BASCO. 1 sire and 26 (4%) of PGS had unknown herd of birth.

Therefore, imported animals, imported semen sires (in the 14299 category) and sires or PGS born outside the UK (in either 14299 or 999999 categories) were removed from the dataset when calculating the influence of UK herds within the herdbook. In calculating PGS born in UK herds, males registered in 2009 with imported sires, imported PGS and PGS in the 14299 quasi herd category were removed from dataset. In this case, removing animals with imported sires therefore removed animals with PGS born outside the UK but not themselves imported, and as such not flagged as imported in BASCO. This calculation assumed no imported bull had a UK born sire, which is supported by the study of Bouquet *et al.* (2011), which found that there was negligible gene flow of pedigree Limousin from the UK to France. From a genetic point of view the actual physical presence of a sire in the UK is not relevant, therefore the two categories of imported father (sire and semen sire) were combined into one figure used to represent imported sires. This was repeated for PGS.

3.2.4. Analysis

A preliminary investigation was undertaken to identify (or otherwise) the presence of an elite group of herds within the pedigree breed. This was done by ranking herds according to the percentage of the 2009 MC which; 1) were born within those herds, 2) were sired by bulls born within those herds, 3) had PGS born in those herds. The influence of top 1, 5 and 10 % of herds for each of these categories was initially quantified. The percentage of herds was calculated according to the number of UK herds registering calves in the mean birth year of each category of animal. There were 1622 herds in 2009, 1543 herds in 2003 (mean year of birth of sires of the 2009 MC) and 1417 herds in 1998 (mean birth year of PGS of the 2009 MC). The

5% proportion was identified as the best descriptor of an elite group, as this was the smallest of the above proportions which bred a majority (52%) of the sires of the 2009 MC. There were 77 (1543 x 0.05) herds in this grouping in 2003. The total numbers in each animal category above were thus calculated for the top 5% of herds in each case**.** The influence of the top 50 herds was also quantified for each animal category.

3.2.5. Selection intensity

The TI was used to determine selection intensity in the pedigree population for terminal traits, which were identified in Chapter 2 as the dominant selection goals in commercial Limousin matings. Ideally the study would have used the TI of parents for the year in which they were (young) selection candidates, in order to identify selection intensity. However, since the complete history of TI was not available, values for parents of the 2010 MC were used, and these were compared with 2009 breed percentiles (the mean year of selection of the parents of the 2010 MC).

In order to give a further indication of the proportion of males selected for use in pedigree breeding per year, the proportion of males born in 2003, which sired any pedigree calves up until 2011, was calculated.

3.2.6. Population genetic merit

The TI was used to compare the genetic merit of animals in the top 5% of herds as defined above (for the 2009 MC), in comparison with breed average herds. TI accuracy was included in this analysis to give an indication of possible bias. Clearly, older sires and those used in larger herds would, typically, have had more recorded progeny than average and thus could have more extreme TI due to greater accuracy alone rather than true genetic merit. Calculating the average TI and TI accuracy for sires and PGS was done using a weighted mean, which took into account the

number of progeny in the 2009 MC per sire and PGS. 2011 TI and TI accuracy values were used in the comparison of the top 5% and breed average herds.

3.2.7. Generation interval

Accurately determining generation interval in a non-controlled population, with regular use of semen sires and imported animals is problematic (Bourbon, 2000). This study therefore uses a simplistic, but typically adopted, definition of generation interval; the mean age of the parents at birth of offspring (the 2009 MC in this study).

3.2.8. Performance recording

Three traits, 400 day weight, calving score and muscle depth were used to give an indication of the levels of performance recording within the breed. The proportion of performance recorded sires was of particular interest, in comparison with the proportion of performance males in the 2009 MC. The two former traits are measured on-farm by the breeder and submitted to BASCO for quality control prior to entry into the database for use in genetic evaluation. While 400 day weight is objectively measured in kg with a weigh scale, calving score is subjectively assessed on a 1 to 5 scale. Muscle depth (of the Longissimus dorsi) is objectively measured by a trained technician, using ultrasound scanning equipment. It should be noted that only UK performance records were available for this analysis, and this will be discussed later in the paper in more detail.

3.3. Results

3.3.1. Calf registrations

Table 3.1 gives a breakdown of 2009 pedigree calf registration for the breed, with 55% of registered calves being female and only 78% of herds' registering (any) male calves. Of herds registering males, only 0.8 % registered 20 or more in 2009 (see also Figure 3.1).

Almost a third of calves are bred using AI, however very few are born as twins or as a result of embryo transfer.

Table 3.1 2009 calf registrations for the UK pedigree Limousin breed

Total number of calves registered	18502
% of registered calves which were male	45
Total number of herds registering calves	1622
Total number of herds (and %) registering (any) male calves	1279 (78%)
Mean number of calves registered per herd	11
% of calves born as twins	2
% of calves bred by AI	31
% of calves born as a result of embryo transfer	3

3.3.2. Generation interval

The male and female generation intervals were 5.6 and 6.2 years respectively, giving an average of 5.9 years.

3.3.3. Performance recording

Of particular note in Table 3.2 is the high proportion of performance recorded sires, compared with the proportion of performance recorded males. For example, the average 2009 born male is 2 times less likely to have a 400 day weight record than its sire. The level of 400 day weight recording in the population has been stable over time, with for example, 28% of males born in 2003 (the mean birth year of sires) having a 400 day weight record, compared with 25% of the 2009 MC. Muscle depth recording has however decreased over the same period, with 0.16 of males born in 2003 measured, compared with only 0.10 of the 2009 MC, a 38% reduction. When this decrease is taken into account by adjusting the sire recording percentage (i.e. by reducing 33 in Table 3.2 column 2 by 38% to give 20.5), sires are still three times more likley to have been scanned than their male progeny born in 2009. Calving score is the most frequently recorded phenotype, with all sires having been scored.

Table 3.2 Percentage of pedigree Limousin males born in 2009 ,and percentage of sires*, with performance records for selected traits with performance records.

	Males born in 2009	Sires* of males born in 2009
Percentage of animals with a recorded 400 day weight	25	51
Percentage of animals with a recorded muscle depth*	7	33
Percentage of animals with a recorded calving score	93	100

*The sire figure describes the percentage of males born in 2009 sired by a bull with a performance record, therefore some sires are counted multiple times.

**Muscle depth recording in the population decreased by 38% for males born in 2009 compared with those born in 2003.

3.3.4. Herd Influence

A minority of herds bred the majority of the 2009 MC (Figure 3.1), with the 50% of the males being born in the top 9% of herds (including all herds registering calves in 2009, ranked by the numbers of males registered per herd). Table 3.3 describes the influence of the top 5% of and the top 50 UK herds, compared with the average UK herd. The top 5% of herds bred 52% of the sires of 2009 born males, with 23 % sired by bulls born outside the UK and the remaining 25% having sires bred in other UK herds. The majority of the 2009 MC (56%) had PGS born outside the UK, with a further 30% having PGS born in the top 5% of UK herds, and the remaining 14% had PGS that were born in other UK herds. The influence of the top 50 herds was found to be broadly similar to that of the top 5% of herds.

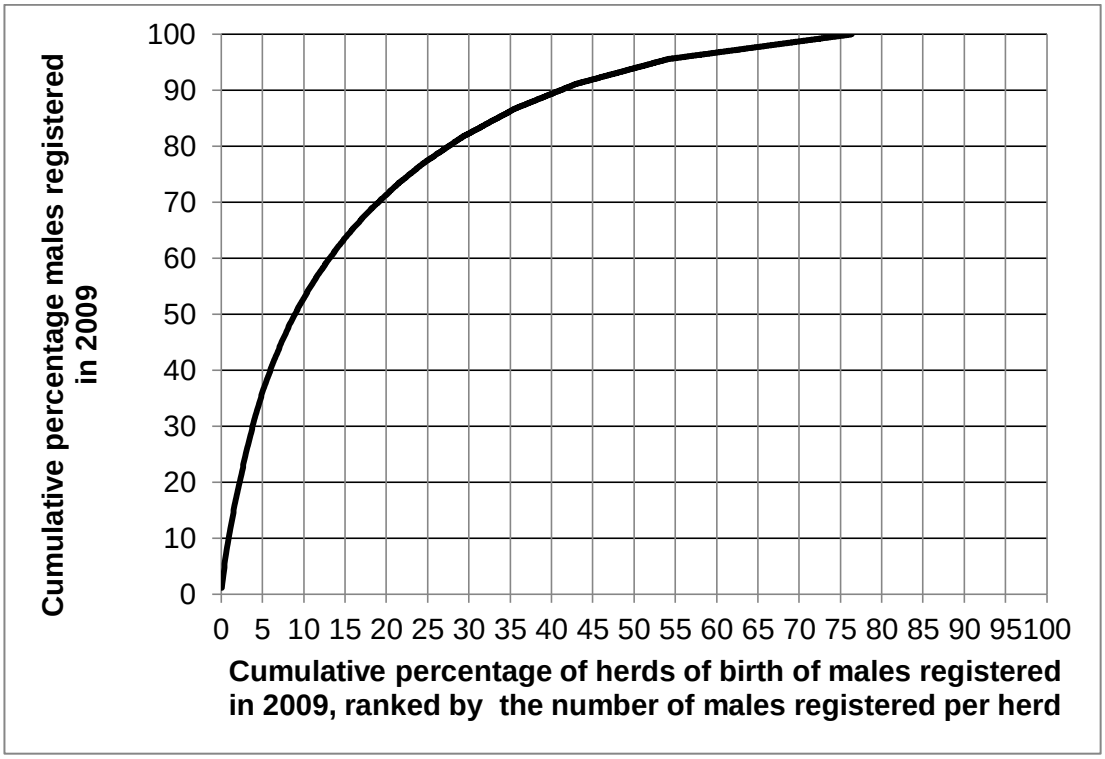

Figure 3.1 Cumulative percentage of herds registering pedigree Limousin males born in 2009, ranked by the number of males registered per herd. [Only 78% of herds registered (any) males].

3.3.5. Sire influence.

When considering influence at the sire level, depicted in Figure 3.2 (which includes non-UK born sires), a similar pattern to that of herd influence (Figure 3.1) is observed. 50% of the 2009 MC was fathered by the most prolific 7% (50) of sires. 77% of males had UK born sires, and 35% of males were sired by bulls born in the top 5% of UK herds (Table 3.3).

Table 3.3 The influence of the top 5% of, and the top 50, UK herds within the UK Limousin herdbook.

Animal	Number of animals	Number of herds of birth of animals	Percentage of imported animals	Percentage of the 2009 MC* born in the top 5% of UK herds**	Percentage of the 2009 MC* born in the top 50 UK herds**
2009 MC*	8270	1279	<1	35	25
			Percentage of the 2009 MC* with an sire, dam or PGS born outside UK	Percentage of the 2009 MC* with a sire, dam or PGS born in the top 5% of UK herds**	Percentage of the 2009 MC* with a sire, dam or PGS born in the top 50 UK herds**
Sire	1537	642	23	52	45
Dam	8067	1237	<1	39	31
PGS	728	346	56	30	27

*The 2009 MC is the cohort of pedigree Limousin males registered in the UK in 2009.
** See Materials and methods for a description of how the top 5% and the top 50 UK herds are selected.

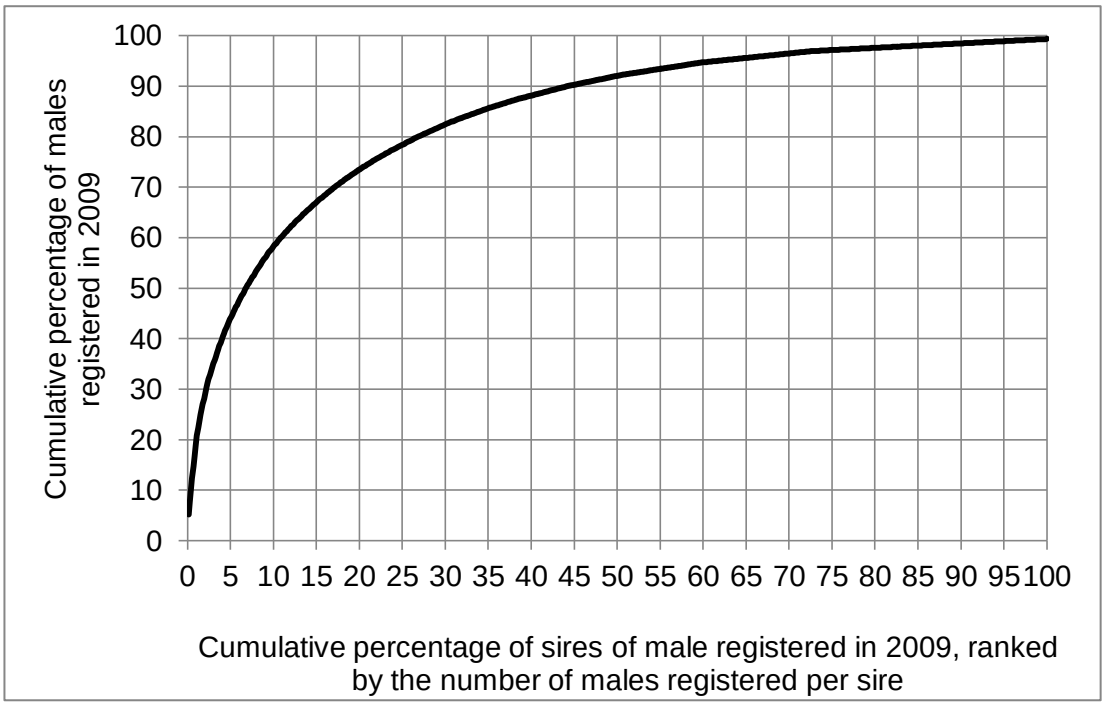

Figure 3.2 Cumulative percentage of all* sires of males born in 2009, ranked by the number of males bred per sire. *Includes sires born outside the UK.

3.3.6. Imported animals

The continuing influence of recently imported bulls and semen is substantial within the UK herdbook (Table 3.3). Almost a quarter of the 2009 MC were sired by bulls born outside the UK, with the majority of these (90%) sired by imported bulls and the remainder (10%) being bred with imported semen. This influence is most evident at the PGS level, with over half the 2009 MC having PGS born outside the UK. When ranked by the number of grandsons in the 2009 MC, 29 of the top 50 PGS were born in France, 20 were born in the UK and 1 was born in Canada**.** The influence of imported genes was similar across elite and breed-average herds, with 24% of males registered by the top 50 herds in 2009 having non-UK born sires, compared with 23% of the entire 2009 MC (Table 3.3).

3.3.7. Selection intensity

The mean TI and TI accuracy of sires and dams of the 2010 MC equated to the 10th and 43rd percentile respectively of the Limousin breed in 2009. These equated to selection intensities of 1.400 and 0.256 s.d. units respectively. 8% of the 2003 MC (613 out of 8005) became sires of (any) pedigree calves, with only 5% (320) siring 10 calves or more, up until 2011.

3.3.8. Genetic merit

Table 3.4 shows mean TI values for the 2009 MC and weighted means for their sires, dams and PGS. The standard deviation of TI values of animals born in 2009 was 7.2. Males born in the top 5% of the 2009 MC, together with their sires and dams, had moderately greater mean TI and TI accuracy than the average of the entire cohort. UK born sires registered by herds outside the top 5% had a mean TI 3.4 points and 0.10 of accuracy less than the mean of top 5% sires. Sires and PGS born outside the UK had greater mean TI, with similar sire TI accuracy and lower PGS TI accuracy than sires and PGS of males born in the top 5% of (UK) herds. Notably, the 14 sires from which semen was imported (fathering 2% of the 2009 MC), had a mean TI of 38.6 (0.98 accuracy), which was equivalent to the top 1 percentile of the breed in 2009. The 29 imported males in the 2009 MC also had a substantially greater TI than average, with Lower accuracy.

Table 3.4 Terminal Index values and their accuracy (in brackets) for pedigree Limousin males registered in 2009 and their sires, dams and PGS, in comparison with animals born in the top 5%* of UK herds.

Animal	Mean TI and (accuracy)	Mean TI and (accuracy) of animals born in the top 5% of UK herds	Mean TI and (accuracy) of animals born in UK herds outside the top 5%	Mean TI and (accuracy) of animals born outside the UK
2009 MC	23.5 (0.59)	25.2 (0.66)	22.5 (0.59)	28.6 (0.49)
	Weighted** mean TI and (accuracy) of sires, dams and PGS of the 2009 MC	Weighted** mean TI and (accuracy) of sires, dams and PGS of the 2009 MC, born in the top 5% of UK herds	Weighted** mean TI and (accuracy) of sires, dams and PGS of the 2009 MC, born in UK herds outside the top 5%	Weighted** mean TI and (accuracy) of sires, dams and PGS of the 2009 MC, born outside the UK
Sire	27.6 (0.84)	28.5 (0.87)	23.2 (0.74)	29.6 (0.87)
Dam	20.0 (0.69)	21.1 (0.73)	19.3 (36.5)	20.8 (0.47)
PGS	27.5 (0.89)	27.1 (0.95)	21.5 (0.82)	28.3 (0.85)

* See Materials and methods for a description of how the top 5% of and the top 50 UK herds are selected.
** The weighted mean takes account of the number of progeny or grand-progeny of the animal in the 2009 MC.

3.4. Discussion

3.4.1. Elite herds

The influence of the top 5% of herds in this study is evidence that an 'elite' group of bull breeding herds exists in the UK Limousin herdbook. In particular, elite herds breed the sires of the majority of the annual male registration cohort. In this aspect, the results of the current study are similar to those observed previously**.** Ozkutuk and Bichard (1977) examined the British and Irish Hereford herdbook, which in the year used in their study (1970), was of similar size to the current UK pedigree Limousin breed. This study found that 33% of the annual Hereford calf cohort was sired by bulls born in influential group of just 0.8% of herds. Similarly, Wiener (1952) estimated that 40.2% of the 1946 British pedigree Ayrshires MC was sired by bulls born in only 3.7% of herds (of herds which bred any sires). Both these studies were conducted at a time before widespread AI use in these breeds (confirmed by the authors). Genes in these herdbooks were therefore entirely disseminated by NS bulls, compared with the current Limousin study, where almost a third of calves were bred with AI. The availability of semen sires from diverse backgrounds, including French based bulls, appears to be one of the factors limiting the influence of the elite herds in this study.

3.4.2. Dissemination of elite breeding

With less than 10% of the 2009 MC likely to be kept as pedigree sires (as evidenced by the 2003 MC), the majority of this pedigree MC will become commercial herd sires in suckler and dairy herds (see Chapter 2). Since half of the MC was born in less than 10% of herds, a considerable proportion of Limousin bulls sold to the commercial breeding sector in the UK are therefore bred in elite herds. Therefore, a

classical multiplier group that is distinct from the 'elite' does not exist in the UK pedigree Limousin population. This is contrary to general animal science theory (Bichard, 1971; Simm, 1998), however as Van Eenennaam and Drake (2012) observed it is generally difficult to quantify this type of structure. The lack of multiplier herds implies a faster rate of dissemination of genetic gain to commercial herds than under conventionally theory. Bichard (1971) for example suggested that a 15 year lag phase existed in UK beef breeding in the 1970's, due to the multiplier tiers in the breeding pyramid. However, the current study provides evidence that only one generation (6yrs) separates the majority of elite Limousin herds and commercial herds (using NS beef bulls).

Chapter 2 found that up to 25% of Limousin NS bulls in commercial herds were pure-bred but non-pedigree registered. This equates to approximately 1500 non-registered replacement sires p.a. The current study sheds light on the origin of these bulls, in that at least 2000 male calves, born in pedigree Limousin herds, were found not to be registered within the herdbook (Table 3.1). While some of these non-registered males, which are probably of lower genetic merit, were reared for slaughter, inevitably a significant portion of these appear to be sold as (cheaper) NS breeding bulls. Dairy herds in particular are potential buyers of these bulls. These herds commonly use NS beef bulls on dairy females not required in breeding replacements (Chapter 2), with the resulting beef cross calves sold at a few weeks of age. In this scenario, farmers simply want a pregnancy (for the cow to resume milk production) and a saleable calf. The added benefits (and cost) of buying a pedigree bull, with for example TI information available, hold little extra value in this case. Non registered bulls, albeit bred in pedigree herd, therefore offer these breeders a cheap NS sire. Furthermore, NS bull rearing is more complex than commercial beef rearing, with bulls requiring halter training, nose-ringing and specialised housing. It is unlikely that any breeders would set up and run exclusively

non-pedigree, pure-bred herds, with the purpose of actively breeding bulls intended for NS, given the extra costs required and the lower returns available (for the herd as a whole) compared with pedigree breeding. In the same way therefore that beef cross dairy calves are a by-product, probably so are many of their sires in practice. Consequently, most non-registered NS bulls likely also disseminate genetic gain from elite through to commercial herds, this time with a two generation lag.

Considering the large influence of Limousin genes in the commercial beef herd, selection decisions in elite pedigree Limousin herds therefore have a major impact on the genetic improvement of terminal traits in the commercial beef herd.

3.4.3. Imported breeding stock

UK pedigree Limousin breeders continue to select considerable numbers of bulls, mainly from France but now also other European countries and North America to use as sires. These bulls are typically of high genetic merit for terminal traits. The massive influence of recently imported French genes in particular, within the UK herdbook, is most evident when examining the origin of PGS. Whilst just under a quarter of the 2009 MC had imported sires (including imported semen), the progeny of those imported sires appear to be preferentially selected as parents of the next generation within the herdbook, with over half of the 2009 MC having PGS born outside the UK. Bouquet *et al.* (2011) found that the UK pedigree population was effectively a smaller 'satellite' population (metapopulation) of the larger French Limousin herd book. Gene flow between France and the UK was unidirectional with 100% of French calves sired by French bred bulls. A more accurate analysis of the genetic influence of French animals could have been achieved by calculating their genetic contributions within UK herdbook. In common with the structure found in the current study, Bouquet *et al.* (2011) further report that 70% of French NS bulls used in pedigree herds are born in a 'nucleus' of 10% of herds, compared with just under

19% in the UK [i.e. 70% of sires (non-weighted) of the 2009 MC were born in 19% of UK herds.

3.4.4. Genetic improvement.

Pedigree Limousin breeders adopt moderate selection intensity for terminal traits in their choice of sires. In comparison, selection intensity in females is low, with breeders needing to retain sufficient breeding cows to produce pedigree males for the commercial NS bull market.

Elite bull breeding herds, as evidenced by the top 5% category in this study, do not employ discernibly greater TI and accuracy than breed-average herds. This is perhaps not surprising given the lack of stratification in the breeding pyramid and the speedy dissemination of improved genes from elite herds, as described above. Furthermore, elite herds constitute a large proportion of animals included in breed average calculation (e.g. over half the sires). When compared with other UK herds therefore, elite herds do appear to use sires with moderately greater TI and accuracy than other UK herds. The genetic merit of elite beef breeding herds and not been greatly studied in the literature. One paper, Koots and Crow (1989), found that Canadian Hereford sires born in elite herds had significantly better EBV for calving ease (the key trait in extensive cattle breeding) than those born in other herds.

An important finding of the current study was that performance recorded bulls are (strongly) preferentially selected over non-recorded bulls for use as pedigree sires (Table 3.1). This is even more evident when considering that imported sires are probably not commonly UK performance recorded at 400 days (most will not have entered the UK before this age). However, these imported sires will almost all have been performance recorded in France, as observed by Bouquet *et al*. (2011) which reported that 92% of French calves are performance recorded at weaning. This

latter figure probably explains the comparatively high genetic merit of imported sires, given the greater emphasis on objective trait recording in France. Given that UK bulls only have EBV data available at breeding sales, it appears likely that performance recording is, in part, undertaken to achieve more accurate and thus greater EBV. This preferential selection of performance recorded sires is therefore further evidence that EBV technology is valued by pedigree breeders.

3.4.5. Generation interval

Bouquet *et al.* (2011) calculated a mean generation interval of 5.9 years for UK pedigree Limousins born in 2000, identical to that estimated in the current study. Figures for French and Irish pedigree Limousin populations in the Bouquet *et al.* (2011) study were 6.1 and 6.3 years respectively. McParland *et al.* (2006) calculated the Irish pedigree Limousin population generation interval to be 6.7 years for animals born in 2004. The heavy use of AI (commonly from French sires) in the development of the Limousin pedigree population in Ireland (Bouquet *et al.* 2011) probably explains the longer generation intervals observed in that population. AI bulls can still sire (many) offspring long after their death, unlike their NS sire counterparts. Although this will increase the generation interval, this can be partially offset by the greater accuracy of older sires' EBV. In fact the French semen sires in this study (mean year of birth 1995) are an example of a group of older AI bulls with a much greater mean accuracy and genetic merit (equivalent to the top 1% of the 2009 MC) than the average sire in the population.

3.4.6. Other breeds

Although Limousin is the dominant player in UK beef breeding, six other beef breeds were shown to have major genetic contributions in Chapter 2. An immediate question must therefore be whether the structure found in this study applies to those

breeds also. Two breeds, Charolais and British Blue (formerly Belgian Blue) were briefly investigated (see Appendix) using publically accessible data (Breedplan, 2012). The influence of (recently) imported animals differs substantially in these herdbooks. While Charolais was the first French imported breed, in contrast to Limousin, this breed now has a much lower use of imported sires. In contrast the British Blue breeding structure is more akin to the Holstein, with international AI sires (mostly Belgian) being heavily used.

3.4.7. Implications for genomic selection

The pedigree herdbook structure described in this study is broadly favourable for GS implementation. Large elite herds, actively using EBV technology, are the driving force behind the rapid dissemination of genetic gain in terminal traits to commercial herds. This has positive implications for the cost effectiveness of GS in UK beef breeding (see also Chapter 4).

Perhaps of most interest however, is the influence of imported genes in UK beef breeding, which may open up major possibilities for GS in the UK. Genotyping Limousin cattle for GS is actively underway in other countries such as France (GEMBAL, 2012) and Canada (Genome Canada, 2012). On the one hand, international genotyping may increase the selection possibilities (and accuracy) for importing breeding animals and gametes. On the other hand, international cooperation could facilitate the development of larger and more predictively powerful genomic training populations (TP), as has occurred in dairy cattle breeding. Indeed, given the huge influence of French genes within the UK herd book, a genomic prediction derived in French Limousin alone could remove the need for a UK Limousin TP altogether. The international possibilities of GS in beef cattle will be investigated in more detail in the General discussion.

3.5. Appendix: an overview of other breeds

Data for both breeds was obtained via the publically accessible Breedplan internet database (Breedplan, 2012).

3.5.1. British Blue.

This is a small UK herd book registering only 895 males in 2010, with a large impact through AI in dairy herds (Chapter 2). The top 20 sires bred 56% of the entire 2010 calf registration, with the top sire alone contributing 8%. Non-UK bred sires (largely through imported semen) fathered 36% of the 2010 MC, with a further 5% of the MC bred by semen from a UK bred bull originally exported to Belgium and whose semen was then imported back to the UK. This is therefore largely an artificially bred breed with a breeding structure more akin to a modern dairy breeds, where a relatively small number of international AI sires are responsible for most of the gene-flow in the breed. However, with its small UK pedigree population below the likely minimum training population requirements for successful terminal genomics (see Chapter 4), this breed could be marginalised by the implementation of UK within-breed genomic programs. However, the strong genetic links created by international AI sires, should allow the UK breed to participate in any future European Belgian Blue genomic project.

3.5.2. Charolais.

The original European import is now very much the smaller cousin, in population terms, compared to its UK Limousin counterpart, with around 3500 pedigree males registered in 2011. This breed has very little commercial AI use, being almost exclusively employed as an NS sire in suckler herds (Chapter 2). In other regards, the structure of the UK Charolais breed is similar to the Limousin. The top 25 herds

(2%), by males registered, bred 25% of the 2011 MC (compared with 3% of the 2009 Limousin MC). The mean terminal index of the herd sires of the top 14 of these herds (by males registered) was equivalent to a top 10% breed value in 2011. The main difference between Limousin and Charolais is the reduced influence of imported sires (and semen) within the breed. For example, only 8% of the 274 Charolais bulls entered in the 2011 February pedigree bull sale in Stirling (the largest Charolais sale in the UK calendar) were sired by a non-UK born bull. (23% of the 2009 Limousin MC were sired by and bull born outside the UK.

Chapter 4:

Genomic selection using beef commercial carcass phenotypes

4.1. Introduction

Chapters 2 and 3 identified pedigree NS bulls to be the main disseminators of improved terminal genetics in cross-breeding commercial suckler herds. In the UK, there is currently no information flow from the performance of commercial progeny of pure-bred bulls, and therefore no inclusion of this data in evaluation of elite breeding populations. The genetic correlation between the performance of the same genes in pure-bred and commercial cross-bred animals (ρ_X) is thus unknown in the UK. Consequently a level of inefficiency, through re-ranking of sires, may be built into evaluations as a result. This problem could be circumvented by including commercial progeny phenotypes in evaluations in combined pure-bred cross-bred selection as described by, for example, Bijma (1998). GS can facilitate this evaluation by establishing genomic links between pure-bred sires used in pedigree and commercial populations. The ideal GS Scenario will therefore be one which most accurately predicts the performance of pure-bred genes in the cross-bred cattle population, as described in the simulation studies of Toosi *et al.* (2009) and Ibanez-Escriche *et al.* (2009).

The aim of this study is therefore to investigate the selection response in terminal traits from a combination of the use of GS with training populations (TP) of varying sizes, made up of single breed NS sires with phenotypes from their commercial progeny. The economic value of this response will also be estimated to inform as to the commercial viability of implementing GS utilising a within-breed TP in the UK.

4.2. Materials and methodology

4.2.1. Breeding goal and index traits.

A TI based on the UK beef value index developed by Amer *et al.* (1998) was used as the selection goal in a deterministic simulation to model the effects of including genomic information in UK beef cattle breeding on response to selection. This index is derived from eleven selection criteria and five goal traits and is constructed as follows:

Eight selection criteria are currently recorded in live pure-bred pedigree animals; birth weight direct (BWT-direct), 200 day weight (WT200), 400 day weight (WT400), muscle score (MSC), fat depth (FD), muscle depth (MD), gestation length direct (GL-direct) and calving difficulty direct (CD-direct). A further three selection criteria, carcass weight (CW), carcass conformation score (CCS) and carcass fatness score (CFS) were assumed for the purposes of this study to be available as recorded phenotypes from abattoirs and represent the potential future recording of commercial carcass phenotypes. These three carcass traits together with the two calving traits (GL-direct and CD-direct) constitute the five goal traits in the existing beef value and in the TI used in this study.

4.2.2. Breeding value convention.

In this study, traditional breeding values which are estimated via BLUP and do not include a genomic component will be referred to as EBV. Genomic breeding values, which are calculated from genomic information only, will be referred to as GBV. In the literature, GBV are sometimes referred to as DGV (direct genomic values). The

combination of EBV and GBV will be referred to as GEBV, where the breeding value is an index of both traditional and genomic information.

4.2.3. Index methodology.

Selection index software developed by Abacus Biotech (NZ) was used to model genetic response in TI from selection when cross-bred phenotypes of slaughter carcass traits are available to create a genomic predictor for selection in the national beef evaluation. In this model, which considers only additive genetic effects, genomic marker information and cross-bred carcass traits were incorporated as correlated traits within a conventional selection index format as per Dekkers (2007a and b), and the philosophy of this approach is outlined in Appendix 1.

In the Dekkers methodology a given trait has separate (but genetically correlated) phenotypic (P) and marker (Q) values. This allows conventional BLUP-derived breeding values to be combined with genomic information for greater accuracy when markers do not capture all of the additive genetic variance. Furthermore, with the assumption in this study that only male selection candidates will be genotyped due to cost considerations, not all pure-bred animals included in evaluations would have GBV information**.** The accuracy of the marker estimated breeding value using the marker data for the component of the genetic value that is associated with the markers ($r_{\hat{Q}}$) for a given trait was predicted following the approach of Daetwyler *et al*. (2008);

$$r_{\hat{Q}} = \sqrt{\frac{\lambda h_o^2}{\lambda h_o^2 + 1}} \qquad (1)$$

In Equation (1) h_0^2 is the heritability of the trait, which in this study is interpreted as the squared accuracy of a progeny test, considering 20 offspring records per sire in

the TP. λ is the number of phenotypes recorded in the TP divided by the number of QTL underlying the trait. In this study the number of genotyped animals was varied from 500 to 20000. The number of QTL affecting the trait was approximated by the effective number of independent segments, following Meuwissen (2009) as;

$$M_e = \sum_{i=1}^{c}(2NeL_i)/\ln(4NeL_i) \qquad (2)$$

Where N_e is the effective population size, C is the number of autosomes (29) and L_i is the length of autosome *i* in the bovine map. Equations (1) and (2) allow the model to be applied with varying effective population size and assuming different sizes of TP. The method allows flexibility in the number of traits in the index and it is possible to include or exclude GBV for individual traits. The index values therefore capture the conventional EBV information and the additional information from the GBVs through the correlations in the index model. The maximum GBV accuracy achievable was set at 0.9 in the model used in this study, in accord with the findings of Daetwyler (2009).

In the current UK Signet genetic evaluations it is assumed that ρ_X is 1.0. In practice it is likely that ρ_X is less than 1.0 (Newman *et al*. 2002; Nunez-Dominguez *et al.* 1993), and therefore sensitivity to ρ_X was investigated by multiplying existing genetic correlations, which are estimated from pure-bred data, by a range of ρ_X values from 0.4 to 1.0. Within each separate Scenario genetic correlations were modified by the same value for ρ_X.

4.2.4. Parameters for modelling.

The UK Limousin breed was used an example population in this study. Phenotypic and genetic parameters for the 8 existing recorded traits comprising the TI were taken from national pedigree evaluations of this breed (see Appendix 2). The three

new recorded commercial carcass traits (CW, CCS and CFS) were assumed to have the same genetic parameters as the existing carcass goal traits, (Table 4.7). It was assumed in this study that these parameters were relevant to pure-breds. Phenotypic correlations for these new traits with existing recorded traits were not available and therefore values identical to the genetic correlations were used. Pure-bred and commercial cross-bred versions of the same trait were also assumed to have identical heritabilities (Appendix 1). Given the need to estimate these parameters used in constructing this model, a weighted bending procedure was incorporated to make the correlation matrices positive-definite (Jorjani *et al*. 2003). The pedigree based estimate of Ne by Bouquet *et al*. (2010) for the Irish Limousin population (a population of similar size and genetic origin to that in the UK), of approximately 300, was adopted for the current study. The bovine autosomal chromosome lengths were taken from Deukwhan and Vasco (2011). Information sources for relatives were parameterized according to the level of performance recording for each trait currently taking place in the UK pedigree Limousin population (BASCO, 2011), (see supplementary material). Generation intervals (5.5 years for males and 6.2 years for females) and proportions of candidates selected (0.2 for males and 0.86 for females) used in the simulations also reflected those currently observed in this population (Chapter 2). These assumptions on generation interval will be discussed later in the paper.

4.2.5. Animals genotyped

It was assumed that genotypes of sires with progeny born in commercial herds would be available to constitute the TP to create the genomic predictor. To fulfil this requirement, male selection candidates in the elite population would be genotyped. Chapter 3 estimated that 320 males from the annual cohort became sires (of 10 or more progeny) in the Elite population. To achieve a selection intensity identified in

Chapter 3, of 1.4 s.d. units under truncation selection, 320/0.2 = 1600 males would need to be genotyped (Following Falconer and Mackay 1996, see Chapter 6 for a more detailed explanation of this calculation). Those males not selected for pedigree breeding would therefore be sold to commercial herds (as per Chapters 2 and 3), and thus provide the information link between commercial and pedigree breeding. The genotyping of imported bulls or semen, many of which are first used (in the UK) as adult bulls (Chapter 3), was not considered at this stage. It is likely that in the genomic era these males would already have been genotyped in their country of origin. The annual Limousin registered cohort consists of less than 1% imported males (i.e. very few bull are imported at a young age). The practical genotyping requirements needed to fulfil these assumptions will be discussed later in the paper.

4.2.6. Scenarios modelled

Three Scenarios were used to investigate the response from incorporating genomic selection and cross-bred phenotypes in the TI evaluations. For each of the Scenarios, responses were calculated for TP sizes of between 500 and 20,000 individuals and for 3 values of ρ_X (0.4, 0.7 and 1.0). GBV was included as an option for selection in males but selection in females was restricted to conventional BLUP-derived EBV only, which reflected the assumption that only male candidates were genotyped. A further Scenario (4) was considered to evaluate the response from a conventional progeny test without GS.

Scenario 1; *Pure-bred*. This Scenario modelled selection for the existing TI comprising of 8 recorded traits. These traits were first evaluated as EBV only i.e. TP = 0, with no genomics which is the equivalent of current gain from BLUP based selection. The impact of combining these EBV with genomic information (GBV) to

produce GEBV for these traits in pure-bred animals was predicted for a range of TP sizes from 500 to 20,000 individuals.

Scenario 2; *Commercial carcass traits*. This Scenario modelled the response when GBV were generated from combining phenotypic carcass records of commercial slaughter animals with genotype information from their pure-bred sires in the TP. In this Scenario the TI includes information from the 3 new recorded commercial carcass traits (CW, CCS and CFS) evaluated as GBV, in addition to the information in Scenario 1.

Scenario 3; *Comprehensive*. This Scenario modelled the combination of Scenarios 1 and 2, with the assumption that GBV were available for commercial carcass traits together with both EBV and GBV for the eight pure-bred recorded TI traits. This Scenario demonstrates what additional benefit over Scenario 2 is obtained from including GBV for the traits currently recorded for existing TI in addition to the conventional evaluation of these traits.

Scenario 4; Conventional progeny test. Response to selection on TI, using a commercial herd progeny test and not using genomics was also investigated. In this case, response was predicted when male selection candidates in the elite pedigree population were assumed to have commercial progeny with phenotypic records for the 3 new commercial carcass traits. Two variations of progeny numbers were considered, 5 and 20. Whilst the latter figure represents an ideal for elite sire candidates, the former is a more realistic number achievable given practical and financial considerations on a pedigree breed wide basis. This progeny test Scenario demonstrates the potential inclusion of commercial carcass traits if the UK were to have a fully comprehensive, traceable and integrated carcass recording system in

place in the beef industry combined with a planned progeny testing programme. The same generation intervals assumed for Scenarios 1 to 3 were also used in this Scenario, and this will be discussed later.

4.2.7. Dissemination of genetic gain to the commercial population

Discounted gene flow was used to estimate the commercial value of genetic improvement to the elite population, following the method of Amer *et al.* (2007). Genetic gain for the five goal traits calculated for the four Scenarios were used as inputs for this model to obtain estimates of financial benefit to the commercial industry. Beef population parameters were adapted from Chapter 2.

A key component of this study was the assumption regarding the proportion of commercial slaughter animals which are sired by bulls with improved genetics. Chapter 2 estimated that at least 75% of Limousin breeding bulls in commercial suckler herds were pedigree. In practice it is likely that the remaining (non-pedigree) Limousin breeding bulls will have been bred in pedigree herds and were not registered as pedigree because they were deemed to be of lower value animals by breeders. Furthermore, the 18% of Limousin progeny which were bred by AI would all have been sired by pedigree bulls. Therefore, this study assumed a 100% dissemination rate of improved genetics, since almost all beef sired animals in the commercial herd are likely to inherit their paternal genes from pedigree bulls and will see the same long term rate of genetic improvement as the elite sector.

A discounting rate of 3.5% (HM treasury, 2012) was used in calculating the net present values associated with the genetic gain predicted from GS. The long term nature of bovine selection was accounted for by calculating cumulative returns over a 20 year period from an initial 10 years of genetic improvement. In the case of this study, this represents the returns from 10 years of investment in selection using genomic information. A genotyping cost of £100 per animal was assumed.

4.3. Results

Scenario 1: Pure-bred. In this case, GS was modelled for purebred traits alone without additional information from commercial phenotypes. The value for gain without GS was £1.01 at TP 0, which corresponds to current gain from BLUP based selection. When GS was used with a TP of 2000 sires and a ρ_X value of 1.0, 5% extra gain was predicted over current selection. Even for larger TP sizes, male selection accuracy remained low in this Scenario (Table 4.1). Considering a lower ρ_X resulted in a reduction in financial responses in TI, however the proportional increase in response with increasing TP size remained the same.

Table 4.1 Terminal index accuracy for male selection in Scenarios 1 to 3 with ρ_X varied.

	ρ_X								
	1.0			0.7			0.4		
Scenario	1	2	3	1	2	3	1	2	3
TP									
0*	0.46	-	-	0.32	-	-	0.18	-	-
500	0.46	0.48	0.49	0.32	0.36	0.37	0.19	0.27	0.27
1000	0.47	0.50	0.51	0.33	0.40	0.41	0.19	0.32	0.33
2000	0.48	0.54	0.55	0.33	0.46	0.46	0.19	0.40	0.40
5000	0.50	0.60	0.62	0.35	0.55	0.56	0.20	0.52	0.52
10000	0.52	0.66	0.68	0.36	0.63	0.64	0.21	0.61	0.61
20000	0.53	0.72	0.73	0.37	0.70	0.70	0.21	0.68	0.68

* TP 0 represents the equivalent of current gain with BLUP based selection.

The predicted response of individual traits within the TI, at $\rho_X = 1.0$ in Scenario 1, is shown in Table 4.2, together with the actual corresponding genetic trends (mean over 5 years) observed in the UK Limousin population (BASCO, 2012). Whilst the overall TI and 400dw predicted gains are similar to actual population trends, greater

muscling, fat and lower calving difficulty are predicted than has been actually observed.

Table 4.2 A comparison of actual UK pedigree Limousin population genetic trends and the responses predicted by the selection index model used in this study when $\rho_X = 1.0$.

Trait	Predicted yearly response (model)	Observed pedigree Limousin population*
400 day weight (Kg)	2.49	1.85 ± 0.05
Muscle depth (mm)	1.41	0.14 ± 0.005
Fat depth (mm)	0.19	-0.005 ± 0.0004
CD direct (%)	0.00	-0.14 ± 0.003
Terminal Index (£)	1.01	0.84 ± 0.02

***** Regression coefficient of Mean EBV, Index with S.E. over the period 2005-2010 (BASCO, 2012).

Scenario 2: Commercial carcass traits. The use of commercial carcass records as phenotypes for TP animals to enable GS in these traits was modelled in this Scenario. The extra gain over Scenario 1 was larger with 15% extra gain with TP = 2000 for $\rho_X = 1.0$. When assuming $\rho_X = 0.7$, the predicted benefit over current gain increased substantially to 38% with TP = 2000. With TP = 5000 this gain increased to 64%. Notable increases in accuracy were predicted for TP greater than 20,000.

Scenario 3: Comprehensive. This represents the combination of information from Scenarios 1 and 2, with GS applied to both pure-bred and commercial carcass traits. Predicted accuracies are of similar magnitude to Scenario 2, with differences reducing as they asymptote. Whilst accuracy is higher with greater ρ_X values, this effect is mitigated with increasing TP size and accuracies gradually converge (Figure 4.1). Marker information alone (i.e. GBV only for all 11 recorded traits) was predicted to give an accuracy of 0.45 (with $\rho_X = 1.0$ and TP = 2000), compared with 0.55 for GEBV.

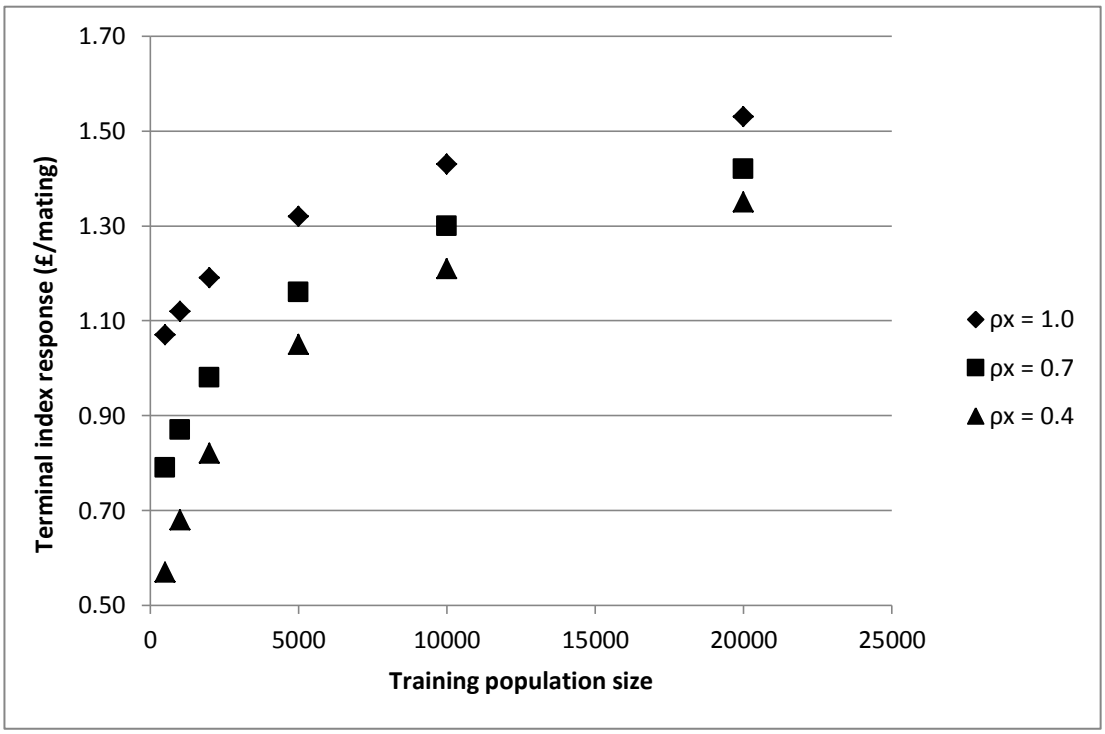

Figure 4.1. Terminal index response (£/mating) for Scenario 3 with ρ_X varied.

Scenario 4: Conventional progeny test. A commercial progeny test without GS was predicted to have a response of £1.23 p.a. per animal, with a male selection accuracy of 0.63 (when ρ_X =1.0) for 5 progeny per elite sire. With 20 progeny these values increase to £1.53 and 0.80 male respectively. The former response is similar to that in Scenario 3 with a TP of 5000, when the comparison is based on accuracy alone without taking into account potential reductions in generation interval possible with GS.

4.3.1. Commercial value.

The cumulative value of genetic gain from 10 years of selection calculated over a 20 year gene flow window, using discounted genetic expressions, from the use of Limousin sires in the UK commercial population is shown in Table 4.3.

Table 4.3 The discounted commercial benefits (£ '000,000) accumulated over a 20 year period, in terminal index gain for Limousin sired prime slaughter cattle, resulting from 10 years of genomic selection in Scenario 3 with ρ_X varied.

ρ_X	1.0	0.7	0.4
TP			
Current gain [1]	30.2	21.0	11.9
500	31.9	23.7	17.0
1000	33.5	27.5	20.1
2000	35.6	29.5	24.9
5000	39.5	34.8	31.4

[1]Current gain equates to BLUP only selection (i.e. no genomic selection in Scenario 1).

Current gain, for 20 years of benefit from 10 years of existing BLUP selection only, was estimated to be worth approximately £ 1.5 million p.a., for ρ_X = 1.0. Using GS resulted in an additional £5.4 million above current selection over 20 years with a TP of 2000 in Scenario 3 and a ρ_X value of 1.0. For ρ_X = 0.7, this benefit increases to £9.4 million.

The value of additional gain minus genotyping costs from GS in Scenario 3 is shown in Table 4.4 and break even genotyping costs are considerably in excess of the £100 per animal assumed in the current study.

Table 4.4 Projected return minus current gain and genotyping costs over a 20 year period, and break even genotyping cost, resulting from 10 years of genomic selection in Scenario 3 with $\rho_X = 0.7$.

Training population size	Net gain from genomic selection (£ '000,000)[1]	Net gain minus genotyping costs (£ '000,000)[2]	Break even genotyping cost (£) per animal[3]
500	2.7	0.9	163
1000	6.5	4.8	382
2000	8.5	6.7	472
5000	13.8	11.7	657

[1] Gain form genomic selection minus current gain in Scenario 1 (from Table 4.3).

[2]Genotyping costs assume £100 per animal in the training population (column 1) and £100 per selection candidate (1600 p.a.) for 10 years. E.g. for a TP of 2000, the number genotyped is 2000 plus (1600 x 10), giving a total of 18,000.

[3]Break even genotyping cost is the additional value of genetic gain minus the value of current gain, from 10 years of genomic selection accumulated over 20 years, divided by the total number of animals genotyped.

4.4. Discussion

4.4.1. Response

This study shows that a synergy between the use of GS and commercial carcass phenotypes has the potential to significantly increase response over current selection terminal beef traits in the UK where cross-breeding is the dominant production system. This benefit is possible even without change in selection intensity or generation interval by UK beef breeders. In addition, the inclusion of more commercially relevant phenotypes in the evaluation of elite pure-bred animals could encourage commercial breeders as a whole to have more confidence in the value of selection indices. Consequently elite breeders may therefore apply greater selection intensity than currently exists in the UK pedigree Limousin population. Although the proportional improvement in genetic gain reported here is independent

of any change in selection intensity, greater total economic benefit would result from increased use of TI by pedigree breeders**.** The results clearly show that implementation of GS with pure-bred records alone would result in little extra gain and would miss major opportunities arising from the inclusion of commercial carcasses phenotypes. However, such opportunities would require the joining up of animal data records from several national and commercial sources; British Cattle Movement Service (BCMS), commercial abattoir databases and pedigree genetic evaluation services. It will also be necessary to genotype sires with commercial progeny, and therefore the establishment of suitable DNA repositories within the breed organisations will be necessary in order to develop suitable TP.

With genomic selection in beef cattle in its infancy, there is limited evidence in the literature with which to compare the responses predicted in this study. Two other simulation studies, Brito *et al.* (2011) and Van Eenennaam *et al.* (2011), predicted increases in accuracy from the use GS in terminal beef traits of similar magnitude to this study. Saatchi *et al.* (2011) reported GBV accuracies of between 0.2 to 0.6 in an actual evaluation of 3570 US Angus bulls, which used deregressed EBV as phenotypes**.** Johnston *et al.* (2012) report GBV accuracy of between 0.25 and 0.47 for carcass traits with a relatively small TP of 1031 genotypes of Australian Angus cattle and an increase in accuracy of 0.04 to 0.06 in GEBV over GBV, when blended. The accuracies predicted in the current study are therefore similar to those found in genomic prediction studies in beef cattle. Whilst the TP levels in these studies were of moderate size, the current study suggests that it may require considerably in excess of 20,000 genotypes to approach the upper end of accuracy achievable with existing SNP panels (Table 4.1).

4.4.2. Estimation of SNP effects

The current study proposes the estimation of SNP effects by genotyping pure-bred bulls and using phenotypes (for carcass traits) from their commercial progeny. In practice, these offspring would most likely be cross-bred in the UK (Todd et al, 2011). Another option would be to genotype the cross-bred progeny directly. Here, the sire genotyping has been preferred as this will deliver unbiased breeding values for pure-bred bulls used as cross-breeding sires even if there is dominance and epistatic variance, whereas using cross-bred data directly can result in biases. As observed by Toosi *et al.* (2009), the accuracy of genomic breeding values can be reduced by the presence of non-additive effects. The bias can be circumvented if it is feasible to identify the parent of origin of the gametes in the cross-breds. This would require additional genotyping and a corresponding increase in cost.

4.4.3. Role of genomics

A key issue with the philosophy adopted in the current study is whether GS is required to achieve the responses in the pedigree population, observed in this study. Theoretically, commercial carcass phenotypes could be used in existing conventional BLUP selection without GS. There are three categories of beef sire which have commercial progeny; AI sires, NS bulls used in commercial herds, and NS bulls used in both commercial and pedigree herds. The commercial progeny of AI sires rarely have sire information recorded in BCMS (Todd *et al.* 2011), and cannot therefore currently be included in genetic evaluations. The offspring of pedigree NS bulls which are only used in commercial herds are effectively the grand-progeny of elite sires in the pedigree population, and it is unrealistic to think that that selection could be made on this basis, given the large generation interval involved. It is not possible to estimate the numbers of NS bulls which have both commercial and pedigree progeny in the UK due to the low level of sire information

in BCMS. Pabiou (2011) suggests that only 1% of pedigree NS sires in commercial herds in Ireland, a country with a very similar beef breeding structure to that in the UK, also have pedigree progeny. It therefore appears unlikely that adequate numbers of elite sires with commercial phenotypes can be included in conventional BLUP evaluation with the existing level of UK animal recording. GS can circumvent this problem by genotyping pedigree bulls and thus establishing DNA relationships between those bulls which end up as sires in commercial herds, and obtain progeny with commercial carcass phenotypes and those which are retained as elite sires in the pedigree sector but have no commercial progeny.

One option to include commercial carcass phenotypes without GS, which would require a restructuring of animal recording, would be a commercial progeny test at the point of selection of elite sire candidates. This study has shown that if 5 commercial progeny per candidate could be recorded, then a response approximately equivalent to GS with a TP of 5000 sire genotypes could be achieved (Scenario 2, $\rho_X = 1.0$). The practicalities of such a progeny test would require three key elements; 1) semen collection of young elite sires which does commonly take place in the UK and 2) laying-off of bulls during their progeny waiting period 3) distribution of this semen to commercial breeders with an incentive to use it within a pre-set timescale and accurately record sire information in cattle passports. The difficulties, both financial and logistic, in achieving points 2 and 3, have meant that large-scale progeny testing has never been adopted in the UK beef industry. Whilst the timescale required for a beef progeny test would be similar to the current generation interval in the Limousin population, it is worth noting that lower generation intervals could be achieved with GS. This Scenario has not been investigated in this study as it would require a substantial change in the practices of elite UK beef breeders.

4.4.4. Economic return

The financial returns estimated in this study are likely to undervalue genetic improvement given that the original beef value TI was calibrated in the early 1990's for a deadweight beef price of around £2/kg (Peter Amer personal communication), rather the £3.50 typically seen in the UK marketplace in 2011-2012 (EBLEX, 2012). Nevertheless, the value of genetic gain from implementation of GS in terminal traits using commercial carcass phenotypes is predicted to be greater than the costs associated with genotyping the TP, even at the lower beef price. Furthermore, this study considered only the 35% of commercial beef progeny which are Limousin sired. Implementing GS across the top 5 beef breeds, accounting for 81% of beef-sired progeny (Todd *et al*. 2011), would increase this return approximately threefold if similar prediction accuracies could be achieved in the other breeds. Implementation costs would also increase proportionately as far as genotyping is concerned unless an effective multi-breed genomic predictor can be developed.

This study predicted the value of current gain in TI from conventional BLUP selection to be considerably greater than Amer *et al.* (2007). That study predicted the combined value of selection across all breeds in the UK to be worth £23 million over 20 years. This equates to only a third of value predicted in the current study, if the Limousin gain was scaled to all other terminal sire breeds in the UK. The difference is largely explained by Amer *et al.* (2007) assuming that terminal improved genes were only disseminated to 30% of the commercial population, which was described as a conservative estimate in that study. In the current study, dissemination to 100% of the commercial population was modelled, with a detailed rationale explained previously in the methodology.

4.4.5. Genomic infrastructure

The size of TP which is practically feasible in UK beef breeds will depend primarily on genotyping costs, NS bull population size and practical issues regarding DNA collection. Given that sires of commercial progeny need to be genotyped (and traced through BCMS), a TP of 5000 would require the genotyping of over half the NS Limousin bulls whose commercial progeny have sire information recorded from the total of UK population of 27,000 NS Limousin bulls and considering approximately 30% of Limousin sired progeny have sire information in BCMS from Todd *et al*. (2011). 2000 genotypes therefore seems a more realistic initial proposition, with the numbers being augmented year on year through re-training and validation of the genomic predictor. This size of TP is projected to be well within the break even genotyping cost estimated in the current study (Table 4.4). In the future it will be more practical to genotype young bulls bred in elite herds before they are sold as commercial sires and this should increase the size of TP practically achievable. Further reductions in costs could be achieved if imputation from lower density SNP panels is feasible (Garrick 2011), an avenue which will require investigation in the UK. Should genotyping costs are fall upon the individual owners of these bulls, it is unlikely to be a barrier to implementation, given the value of elite beef bulls (measured in £1000's; BLCS, 2012) and the falling costs of genotyping (measured in £100's). Furthermore, the potential revenue from sales of semen from these bulls is likely to be enhanced with availability of DNA information, particularly in export markets.

Given the NS bull population estimates in Chapter 2, four other UK breeds are likely to have the numbers of bulls required (and adequate level of sire information in BCMS) for a TP of 2000, namely; Charolais, Simmental, Angus and Hereford. Although Belgian Blue was estimated to have the fifth largest contribution to prime slaughter genes in Chapter 2, this was mostly through AI and consequently, only 9%

of sires were recorded in BCMS. Even if the sire recording rate matched that of other breeds (i.e. around 25 to 30%) for the progeny of the estimated 3600 NS bulls in the commercial population, almost all sires suitable for a genomic evaluation would be need to be genotyped to achieve a TP of just 1000 animals. As observed by Garrick (2011), if effective multi-breed SNP panels are not developed, breeds with small pedigree populations could be marginalised by GS.

4.4.6. Adequacy of the model

The selection index model used in this study was parameterized as far as possible with actual pedigree Limousin population data, however assumptions were necessary for certain parameters which were unavailable. In particular, identical phenotypic and genetic correlations were used for carcass traits. Gregory *et al*. (1995) reported phenotypic and genetic correlations between carcass weight and carcass fat of 0.67 and 0.51 respectively. Similarly, Hickey *et al.* (2007) reported values of 0.22 and 0.26 for the same parameters. Therefore, although the magnitude of these correlations varies across studies (depending on factors such as breed), the relative difference between phenotypic and genetic correlations within study are small, suggesting that the assumption in the current study was a reasonable first approximation. A further assumption was made in ρ_X variations, with all traits being modified by the same ρ_X value. In practice it is likely that different groups of traits will display varying magnitudes of genotype by environment interactions (Nunez-Dominguez *et al*. (1993). However, TI response was shown in the current study to be largely driven by one trait, 400 day growth (Table 4.2). Therefore, the value of ρ_X for this trait will dominate the predictions and deviations from this value in other traits will be unlikely to have major consequences on selection response predictions. Nunez-Dominguez (*et al.* 1993) provided estimates

of ρ_X for 365 day weight averaging 0.77, and therefore $\rho_X = 0.7$ is probably the most relevant value used in the current study. Importantly, the cross-bred evaluation envisaged in the current study would provide insight into this key parameter in the UK.

Whilst the overall TI response is very similar between the model and what is observed, some of the predicted trait responses are different from those observed currently (see Table 4.2). The model simulates selection for the TI and this has resulted in greater response in muscling traits than that actually observed in the UK Limousin population. In contrast, calving difficulty (CD direct) has virtually no response in the model whereas this trait has a negative genetic trend in the UK Limousin population. With only moderate uptake of the TI index (Todd *et al*. 2011), clearly certain individual traits, such as muscle depth, may be less strongly selected in practice than is reflected by their economic weighting in the TI. This may be due to a continued reliance, by some breeders, on visual appraisal of carcass characteristics in elite selection candidates. This model therefore represents an idealised selection, which nonetheless results in a very similar overall TI response. The model does however predict that current TI gain could be achieved without undesirable reductions in calving ease, through a comprehensive use of EBV and index technology.

4.7. Conclusion

In proportional terms, the additional response from the inclusion of GS and commercial carcass phenotypes was considerable, particularly when considering a realistic ρ_X of 0.7 and a feasible TP size of 2000. The increase in genetic gain predicted is similar to that observed in TI after the introduction of BLUP EBV in UK beef evaluations. The commercial value of this extra gain is estimated to be

substantially in excess of current genotyping costs. Implementation using commercial carcass phenotypes in terminal traits could provide the financial platform for GS in other traits. Importantly, the scheme described in this study does not require major change in UK beef breeding practices.

Obtaining relevant sire genotypes is likely to be the main practical obstacle to GS implementation in the beef sector. To overcome this issue, those breed organisations considering future adoption of GS would be advised to implement a comprehensive program of DNA collection of young bulls before their sale to commercial herds.

4.8. Appendices

4.8.1. Appendix 1

Table 4.5 Construction of (Co)variance matrices, assuming all phenotypic variances (P1, P2, P1cp and P2cp) are scaled to 1. Phenotypic covariance on upper diagonal, genetic covariance below and genetic variance on diagonal.

	P1	P2	P1cp	P2cp	Q1	Q2	Q1cp	Q2cp
P1	h_1^2	ρ_P	ρ_x	$\rho_P\rho_X$	$h_1^2q^2r_1^2$	$h_1^2h_2q^2r_2^2\rho_G$	$h_1^2q^2r_1^2\rho_X$	$h_1^2h_2q^2r_2^2\rho_G\rho_X$
P2	$h_1h_2\rho_G$	h_2^2	$\rho_P\rho_X$	ρ_X	$h_1h_2^2q^2r_1^2\rho_G$	$h_2^2q^2r_2^2$	$h_1h_2^2q^2r_1^2\rho_G\rho_X$	$h_2^2q^2r_2^2\rho_X$
P1cp	$h_1^2\rho_X$	$h_1h_2\rho_G\rho_X$	h_1^2	ρ_P	$h_1^2q^2r_1^2\rho_X$	$h_1^2h_2q^2r_2^2\rho_G\rho_X$	$h_1^2q^2r_1^2$	$h_1^2h_2q^2r_2^2\rho_G$
P2cp	$h_1h_2\rho_G\rho_X$	$h_2^2\rho_X$	$h_1h_2\rho_G\rho_X$	h_2^2	$h_1h_2^2q^2r_1^2\rho_G\rho_X$	$h_2^2q^2r_2^2\rho_X$	$h_1h_2^2q^2r_1^2\rho_G$	$h_2^2q^2r_2^2$
Q1	$h_1^2q^2r_1^2$	$h_1h_2q^2r_1^2\rho_G$	$h_1^2q^2r_1^2\rho_X$	$h_1h_2q^2r_1^2\rho_G\rho_X$	$q^2r_1^2h_1^2$	$h_1h_2r_1^2r_2^2\rho_G$	$h_1^2r_1^2\rho_X$	$h_1h_2r_1^2r_2^2\rho_G\rho_X$
Q2	$h_1h_2q^2r_2^2\rho_G$	$h_2^2q^2r_2^2$	$h_1h_2q^2r_2^2\rho_G\rho_X$	$h_2^2q^2r_2^2\rho_X$	$h_1h_2r_1^2r_2^2\rho_G$	$q^2r_2^2h_2^2$	$h_1h_2r_1^2r_2^2\rho_G\rho_X$	$h_2^2r_2^2\rho_X$
Q1cp	$h_1^2q^2r_1^2\rho_X$	$h_1h_2q^2r_1^2\rho_G\rho_X$	$h_1^2q^2r_1^2$	$h_1h_2q^2r_1^2\rho_G$	$h_1^2r_1^2\rho_X$	$h_1h_2r_1^2r_2^2\rho_G\rho_X$	$h_1^2q^2r_1^2h_1^2$	$h_1h_2r_1^2r_2^2\rho_G$
Q2cp	$h_1h_2q^2r_2^2\rho_G\rho_X$	$h_2^2q^2r_2^2\rho_X$	$h_1h_2q^2r_2^2\rho_G$	$h_2^2q^2r_2^2$	$h_1h_2r_1^2r_2^2\rho_G\rho_X$	$h_2^2r_2^2\rho_X$	$h_1h_2r_1^2r_2^2\rho_G$	$q^2r_2^2h_2^2$

Pure-bred (P) and commercial cross-bred (Pcp) performance and pure-bred (Q) and commercial cross-bred (Qcp) marker-based EBV.

Table 4.5 exemplifies the methodology for the construction of the (co)variance matrices, using two traits measured on both pure-bred and commercial cross-breds, where the phenotypes have been standardised to have a phenotypic variance of 1.

The genetic correlation in pure-bred sires between traits i and j measured in pure-breds is ρG and this is assumed to be the same when the breeding values are for i and j measured in cross-breds. However the correlation between a breeding value for pure-bred performance in i and cross-bred performance in the same trait i is assumed to be ρX, the same for all traits, due to lack of information. The correlation between breeding values for trait i as a pure-bred and trait j≠i as a crossbred is assumed to be ρGρX. This implicitly assumes the independence of the cross-bred breeding value for trait j and the pure-bred breeding value for trait i given the pure-bred breeding value for trait j, i.e. the best prediction of cross-bred breeding values from pure-bred breeding values is given by the pure-bred breeding value of the same trait. Further, it is assumed that: (i) the variance of breeding values for trait i is the same for pure-bred and cross-bred performance when phenotypes are scaled to have variance 1, i.e. in Table 4.5, h2 for trait i is the same in pure-breds and cross-breds. In Table 4.5, ρP indicates a correlation between the phenotypes if i and j, which was also assumed to be the same in pure-breds and cross-breds. The accuracy of the marker estimated breeding value for trait i using the marker data for the component of the genetic value that is associated with markers r_i for a given trait was predicted following the approach of Daetwyler *et al.* (2008). The marker genotyping panel is expected to capture a fraction q2 of the genetic variance in the traits (Daetwyler, 2009), and this was assumed to be the same for all traits, which means the maximum accuracy obtainable for a genomic predictor for the observed traits is q. In this study q was assumed to be 0.9.

4.8.2 Appendix 2.

Table 4.6 Existing and new recorded traits in the terminal index.

Recorded trait name[1]	Heritability	Phenotypic Variance
BWT-direct[1], kg	0.23	9.0
WT200[1], kg	0.33	807
WT400[1], kg	0.40	1589
MSC[1], score (1-15, higher = higher muscularity)	0.27	1.3
FD[1], mm	0.29	6395
MD[1], mm	0.26	2518
GL-direct[1], days	0.29	23.8
CD-direct[1], score (1-5, higher = increased assistance required)	0.12	1.0
CCW[2] ,kg	0.44	859
CCCS[2], score	0.11	9.8
CCFS[2], score	0.13	4.1

[1]Definition of trait name abbreviations of existing TI traits : BWT, birth weight; WT200, weight at 200 days; WT400, weight at 400 days; MSC, muscle score; FD, fat depth; MD, muscle depth; GL, gestation length; CD, calving difficulty;

[2]New recorded traits included in the index: CCW, cross-bred carcass weight; CCCS, cross-bred carcass conformation score; CCFS, cross-bred carcass fat score.

Table 4.7 Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations between existing and new recorded traits in the terminal index. (ρ_X =1.0)

	BWT-direct	WT200	WT400	MSC	FD	MD	GL-direct	CD-direct	CW	CCS	CFS
BWT-direct	1.00	0.50	0.41	0.38	0.09	0.47	0.55	0.58	0.15	0.15	0.00
WT200	0.27	1.00	0.85	0.42	0.22	0.60	0.10	0.29	0.50	0.18	0.08
WT400	0.19	0.85	1.00	0.53	0.12	0.55	0.05	0.10	0.60	0.20	0.10
MSC	0.10	0.48	0.43	1.00	0.00	0.63	0.19	0.07	0.30	0.60	0.00
FD	0.05	0.17	0.22	0.16	1.00	0.18	0.00	0.05	0.10	0.10	0.40
MD	0.10	0.32	0.43	0.49	0.16	1.00	0.20	0.10	0.30	0.60	0.10
GL-direct	0.20	0.07	0.00	0.12	0.00	-0.01	1.00	0.21	0.10	0.10	0.00
CD-direct	0.31	0.02	0.03	0.01	0.00	0.00	0.11	1.00	0.10	0.10	0.00
CW	0.15	0.50	0.60	0.30	0.10	0.30	0.10	0.10	1.00	0.00	0.00
CCS	0.15	0.18	0.20	0.60	0.10	0.60	0.10	0.10	0.00	1.00	0.10
CFS	0.00	0.08	0.10	0.00	0.40	0.10	0.00	0.00	0.00	0.10	1.00

Definition of trait name abbreviations: BWT, birth weight; WT200, weight at 200 days; WT400, weight at 400 days; MSC, muscle score; FD, fat depth; MD, muscle depth; GL, gestation length; CD, calving difficulty; CW, carcass weight; CCS, carcass conformation score; CFS, carcass fat score.

Table 4.8 Heritability, phenotypic variance and economic weights for profit traits in the terminal index.

Profit trait name[1]	Heritability	Phenotypic variance	Economic weight (£)
CW, kg	0.44	860	1.2
CFS, score (1-15)	0.13	4.10	-6
CCS, score (1-15)	0.11	9.83	7
GL-direct, days	0.29	23.81	-1
CD-direct, (score 1-5)	0.12	1.02	-2.88

[1]Definition of trait name abbreviations: CW, carcass weight; CFS, carcass fat score; CCS, carcass conformation score; GL, gestation length; CD, calving difficulty.

Table 4.9 Estimates of genetic correlations between existing and new recorded traits and profit traits in the terminal index.

	CW	CFS	CCS	GL-direct	CD-direct
BWT-direct	0.15	0.00	0.15	0.55	0.58
WT200	0.50	0.80	0.18	0.10	0.29
WT400	0.60	0.10	0.20	0.05	0.10
MSC	0.30	0.00	0.60	0.19	0.07
FD	0.10	0.40	0.10	0.00	0.05
MD	0.30	0.10	0.60	0.20	0.10
GL-direct	0.10	0.00	0.10	1.00	0.21
CD-direct	0.10	0.00	0.10	0.21	1.00
CW	1.00	0.00	0.00	0.10	0.10
CCS	0.00	1.00	0.00	0.10	0.10
CFS	0.00	0.00	1.00	0.00	0.00

Definition of trait name abbreviations: CW, carcass weight; CFS, carcass fat score; CCS, carcass conformation score; GL, gestation length; CD, calving difficulty; BWT, birth weight; WT200, weight at 200 days; WT400, weight at 400 days; MSC, muscle score; FD, fat depth; MD, muscle depth; CW, carcass weight; CCS, carcass conformation score; CFS, carcass fat score.

Table 4.10 Estimates of genetic correlations between profit traits in the terminal index

	CW	CFS	CCS	GL-direct	CD-direct
CW	1.00	0.00	0.00	0.10	0.10
CFS	0.00	1.00	0.00	0.00	0.00
CCS	0.00	0.00	1.00	0.10	0.10
GL-direct	0.10	0.00	0.10	1.00	0.21
CD-direct	0.10	0.00	0.10	0.21	1.00

Definition of trait name abbreviations: CW, carcass weight; CFS, carcass fat score; CCS, carcass conformation score; GL, gestation length; CD, calving difficulty.

Table 4.11 Information sources used in the model, based on pedigree Limousin data from BASCO (2012).

Information source name[1]	Number of animal records (Male)	Number of animal records (Female)
BWT-direct (on candidate)	1	1
BWT-direct (on paternal half-sibs)	3	3
WT200-direct (on candidate)	1	1
WT200-direct (on paternal half-sibs)	4	4
WT400 (on candidate)	1	1
WT400 (on paternal half sibs)	3	3
MSC (on candidate)	0	0
MSC (on paternal half sibs)	1	1
FD (On candidate)	0	0
FD (On paternal half sibs)	1	1
MD (on candidate)	1	1
MD (on paternal half sibs)	1	1
GL-direct (on candidate)	1	1
GL-direct (on paternal half sibs)	5	5
CD-direct (on candidate)	1	1
CD-direct (on paternal half sibs)	16	16
BWT (on progeny)	8	1
WT200 (on progeny)	8	1
WT400 (on progeny)	6	1
MD (on progeny)	2	1
FD (on progeny)	2	1
MSC (on progeny)	0	1
GL (on progeny)	10	1
CD (on progeny)	33	1
CCWT (on progeny) [2]	20	0
CCCS (on progeny) [2]	20	0
CCFS (on progeny) [2]	20	0

[1]Definition of trait name abbreviations: BWT, birth weight; WT200, weight at 200 days; WT400, weight at 400 days; MSC, muscle score; FD, fat depth; MD, muscle depth; GL, gestation length; CD, calving difficulty.

[2]Traits used only in the conventional progeny test simulation: CCWT, commercial carcass weight, CCCS, commercial carcass conformation score and CCFS, commercial carcass fat score.

Chapter 5:

Genomic selection in maternal beef traits

5.1. Introduction

A major attraction of genomic selection (GS) in dairy cattle breeding has been the opportunity to increase genetic gain through a reduction in generation interval of AI sires (Schaeffer, 2006). In the beef industry, young bulls are predominantly selected as natural service (NS) sires, typically at less than two years of age (Chapter 2). Terminal traits can be assessed at a relatively young age in beef breeding bulls, through performance recording, and these traits are not sex limited. As explored in Chapter 4, this breeding system is moderately effective in selecting for terminal trait goals. In contrast, maternal traits [which in this Chapter will be restricted in definition to fertility, calving ease, lifespan and 200 day milk (200 day weight maternal rearing effect)] are both sex and age limited, not being expressed until daughters of bulls begin reproducing themselves. Consequently, young beef sire EBV for maternal traits are calculated from parent average information only, and the resulting accuracies are low in comparison with those for terminal trait EBV (Moore *et al*, 2010; BASCO, 2012). One option to overcome this problem would be to implement formal progeny testing (PT) of selection candidates. France is an example of a country which adopted this route with state-run maternal PT in major beef breeds (Phocas and Sapa, 2004). This system was supported by wide scale use of maternally tested AI bulls by French commercial breeders, with for example about one third of pure-bred Charolais calves bred by AI (Bouquet *et al*. 2010). It is worth noting that commercial suckler herds in France largely employ pure-breeding, which increases the relevance of pedigree phenotypes compared with the UK. As discussed in Chapters 2 and 3, large scale PT of beef sires has never been adopted in the UK.

5.1.1. UK maternal structure

In Chapter 2 it was estimated that around 40% of suckler cows in the UK are of beef cross dairy breed origin, effectively a by-product of the dairy herd. Although the remainder have both a beef sire and a beef maternal grandsire, many will still have a component of dairy genetics in their makeup. Only 12% of the progeny of beef-sired matings are retained for breeding, with the remainder being slaughtered for prime beef. This figure reduces to 7% if only suckler herd matings (beef x beef) are considered. These novel findings explain much of the dominance of terminal trait goals observed in UK beef breeding. It is commonly suggested that selection for terminal goals can lead to deterioration in some maternal traits expressed by suckler cows (e.g. Amer *et al.* 1996; Roughsedge *et al*. 2005a). For example, the genetic correlation between 400 day weight, a key terminal trait, and maternal calving ease is -0.34 in the Limousin breed.

Against this background, most maternal traits, for which conventional EBV are evaluated, do not show evidence of selection (through genetic trends) at a population wide level (as discussed in Chapter 2). Figure 5.1 depicts these trends in the Limousin breed. Lifespan (LSP) does show an increase in EBV since 1995, during the period over which the BSE disease epidemic occurred in the UK. Between 1995 and 2006, adult cows aged over 30 months at death could not enter the human food chain and as such had very low slaughter value of around £200 (Roughsedge *et al.* 2005a), which is less than a quarter of their typical market value in 2012 (EBLEX, 2012). Breeders may therefore have retained fertile cows to a greater age (than pre 1995 and post 2006) in order to maintain the lifetime production value of these animals. Whilst BLUP has the capacity to adjust EBV for environmental variations year on year, no specific correction was implemented in BASCO evaluations to account for any altered selection by breeders during BSE (Kirsty Moore, personal communication). Furthermore, the Lifespan EBV was first

introduced only in 2006. These circumstances therefore cast doubt on whether the Lifespan EBV trend is evidence of active selection for longevity.

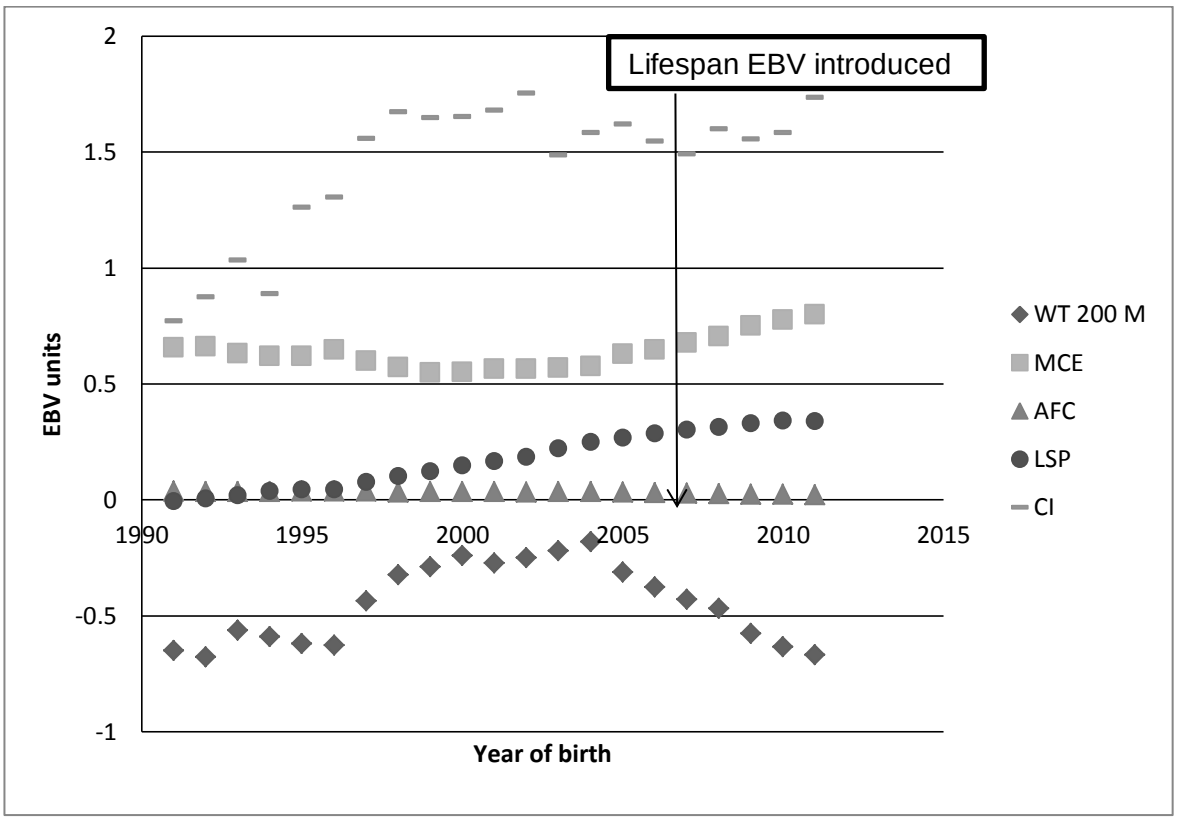

Figure 5.2 EBV trends in the Limousin breed for the five component traits of the Maternal Value selection index (Signet, 2012). Trait description; lifespan (LSP), age at first calving (AFC), calving interval (CI), 200 day weight-maternal (WT 200M) and maternal calving ease (MCE), (Data from BASCO, 2012).

It should be noted that MCE, AFC and CI have negative economic weightings (Table 5.3), and therefore an upward genetic trend is undesirable in these traits.

5.1.2. Maternal selection Indices.

Two selection indices, which include maternal traits, are currently available for the pedigree Limousin breed (Signet, 2012):

1) Maternal value (MV); which is comprised of five key maternal profit traits; lifespan (LSP), age at first calving (AFC), calving interval (CI), maternal calving ease (MCE) and 200 day weight-maternal (WT 200 M) [which is sometimes referred to as '200 day milk' in the literature].
2) Maternal production value (MPV); which is the MV plus some terminal and maintenance goal traits. This index reflects a rounded selection goal, acknowledging that progeny inherit half their terminal trait genes from their dam (Roughsedge *et al*. 2005). However, as the economic weighting of cow maintenance value, used in the index calculation, has not been updated to reflect the return of cull cow beef in the human food chain since 2006 (Defra, 2006), the current relevance of this index is questionable.

Maternal traits tend to be of lower heritability than growth and carcass traits, such as those modelled in Chapter 4. This can pose problems when selecting for a composite (maternal plus terminal traits) index such as MPV, which tend to be primarily driven by the higher heritability (terminal) traits. This often occurs at the expense of deterioration in some maternal traits, as observed by Roughsedge *et al.* (2005). MPV could therefore show improvement without any gain in maternal traits.

5.1.3. Active selection strategy.

In Chapter 3, evaluating the implementation of GS in terminal traits relied upon an estimate of selection intensity observed in the population. However, it appears that selection intensity is very low for maternal traits in UK beef breeding (as demonstrated for example by the Limousin breed). A more active strategy is

therefore required when considering implementation of GS in UK maternal beef traits. It is likely that breeders within individual herdbooks, interested in breeding bulls for maternal goals, would have to combine resources in a cooperative breeding scheme such as that employed by the UK Stabiliser breed group for example (Big Beef, 2012). This would allow breeders to achieve greater selection intensity and develop a nucleus of elite stock with above breed-average maternal EBV.

The aim of this study was therefore to explore the viability of GS for beef maternal traits, using a maternal selection index, when adopted by a nucleus group of beef breeders actively selecting for maternal traits. In particular, the relative merits of GS were compared with PT and (active) BLUP selection, within the nucleus herd format. The use of commercial phenotypes (such as modelled in Chapter 4) was not proposed in this study, as phenotypes for most maternal traits are not recorded (e.g. in BCMS) in commercial suckler herds.

5.2. Materials and methods

5.2.1. Data

The Limousin breed was used as an example population with which to model GS and PT selection within a maternal nucleus. This breed, which has a breeding female population of approximately 32,000 pedigree cows (BASCO, 2012), was shown to contribute the most beef genes to the commercial suckler cow population in Chapter 2. Phenotypic and genetic parameters for maternal and terminal traits, estimated by Roughsedge *et al.* (2005b) and Amer *et al.* (1998) respectively, were used in this study (see Appendix Tables). Pedigree and commercial population parameters estimated in Chapters 2 and 3, were adopted in this study, and are described in detail in the following sections.

5.2.2. Breeding goal

A maternal selection index (MI), based on the MV index described above, was used as the breeding goal in a deterministic simulation to model nucleus maternal breeding. The MI was composed of thirteen recorded traits. The five maternal traits included in MI were; maternal calving difficulty, calving interval, age first calving, lifespan, and 200 day weight-maternal (which is sometimes referred to as 200 day milk in the literature). These five maternal traits were also used as profit traits in the simulation, and their economic weights are shown in Table 5.3. Eight terminal traits were also included in the MI, with zero economic value, to estimate the correlated effect on terminal traits, of selection for maternal goals. The terminal traits included were; birth weight, weight at 200 days, weight at 400 days, muscle score, fat depth, muscle depth, gestation length and calving difficulty. All traits would be recorded on live pedigree animals.

5.2.3. Breeding value convention

The breeding value convention used in chapter 4 was also adopted in this chapter, and is as follows; Traditional breeding values which are estimated via BLUP and do not include a genomic component will be referred to as EBV. Genomic breeding values, which are calculated from genomic information only, will be referred to as GBV. In the literature, GBV are sometimes referred to as DGV (direct genomic values). The combination of EBV and GBV will be referred to as GEBV, where the breeding value is an index of both traditional and genomic information.

5.2.4. Index methodology

A deterministic simulation, using the same model which is described in detail in Chapter 4, was used to predict response and accuracy for MI in each of three scenarios (described in detail below). When modelling MI selection, it assumed that

the genomic predictor would be calculated using a training population (TP) comprised of pedigree animals with phenotypes for maternal traits derived from their deregressed EBV (Mrode, 2005)**.** This approach has been adopted for example in US Angus GS (Garrick, 2011). Only pure-bred simulations were considered, and Identical Ne and chromosome lengths to those adopted in Chapter 4, were used in this simulation.

5.2.5. Scenarios modelled

Response to selection with the concept of maternal nucleus group of herds was evaluated by comparing three different strategies;

1) **BLUP**. Young sires selected on the basis of MI composed of traits calculated as EBV only, at an early breeding age (1.5 years) and used across the nucleus herds.

2) **YSG**. Young sires selected on MI with GEBV**,** initially across the entire population, at an early breeding age (1.5 years) and used across the nucleus herds.

3) **PT**. A progeny test scenario evaluating between 20 daughters per bull, within nucleus herds. Proven sires would be chosen for selection on the basis of MI composed of traits calculated as EBV only, at 6 years of age, which reflects the timescale required to evaluate the first and second calving of daughters. This would allow for estimation of the calving interval phenotype.

The nucleus schemes are summarised in Table 5.1. The aim of these schemes would be to produce young NS bulls, with improved maternal traits, for sale to commercial farmers.

Table 5.1. Details of proposed maternal nucleus scenarios.

Scheme	Number of daughters evaluated per bull*	Proportion of males selected	Proportion of females selected	Male generation interval
BLUP (Conventional young sire EBV)	-	0.005 or 0.05	0.50	3
GYS (Genomic young sire)	-	0.005 or 0.05	0.50	3
PT (Progeny test with EBV)	20	0.005 or 0.05	0.50	6

* Number of daughters evaluated per bull applies in the progeny test only.

5.2.6. Nucleus format

The assumptions regarding the size and make-up of the nucleus herd group were intended to reflect the practicalities of such as scheme, as well as the motivation of breeders to participate. It was considered that the number of herds willing to participate in such a scheme would reflect the numbers of breeding females required to supply NS bulls with improved maternal genes to the commercial suckler population. As this study constitutes a preliminary exploration of nucleus breeding, the numbers of animals used in the calculations in this section are not intended be definitive.

In Chapter 2 (Table 2.5) it was estimated that about 10 % of Limousin-sired matings p.a. resulted in a female retained for commercial breeding (Table 2.7), and that approximately half of these matings occurred in the dairy herd. As discussed in Chapters 2 and 3, calves born from beef x dairy matings are by-products of milk production, generally sold at just a few weeks of age, and as such there would be no reason for their sires to be selected for maternal beef traits. The other 5% of

Limousin-sired matings resulting in replacement suckler females therefore occur in the beef suckler herd, mainly via NS sires. These bulls are therefore those which could in theory be selected for maternal goals (this calculation ignores the small proportion of AI in the commercial suckler herd). It was considered unlikely that semen collected in this scheme would be sexed, given the relatively small amount of required and the extra cost involved with this method (Telford *et al.* 2003). Half the matings intended to breed replacement females would thus produce a male calf. Therefore, in order to achieve 5% maternal matings, 10% of Limousin-sired matings would need to involve bulls selected for maternal goals. Assuming that this 10% value represents the maximum size of the NS bull market for maternal sires, it seems reasonable to assume that this figure also represents the maximum proportion of pedigree Limousin breeders who would be willing to participate in a nucleus maternal breeding scheme. Consequently, a maternal nucleus size of 3200 females (10% of 32,000) was adopted for the maternal scenario simulations.

In the case of the PT scenario, it was considered that only half (1600 females) of the nucleus could realistically be used for PT, with the remaining females mated to the best proven sires from the PT to produce NS bulls for sale to commercial suckler herds. Assuming that 75% of female calves born to the 1600 females in the PT nucleus would be reared to breeding age of approximately 2yrs (see Appendix in Chapter 2), would produce 600 (1600 / 2 x 0.75) potential daughters of PT sires. An aim of 20 daughters being tested per bull would thus allow 30 bulls to be tested per year.

5.2.7 Selection intensity

Male. From the 30 bulls used in PT per year, 6 proven sires would be selected each year for use (via conventional AI) in the non-PT half of the nucleus. Using the same rationale as above, a nucleus of 3200 females would produce 1200 male selection

candidates p.a. (3200 / 2 x 0.75). Selecting the best 6 sires (for example) p.a. from this group, would give a male proportion selected of 0.005 (6 / 1200)**,** and in theory achieve a very high male selection intensity of greater than three standard deviations above breed average. However, in practice, cattle PT schemes typically only achieve a selection intensity of about one standard deviation above breed average (Fouilloux *et al.* 1999; Powell *et al.* 2003). Clearly, it is difficult to accurately the highest genetic merit candidates for the progeny test, based on parent average EBV, particularly when considering the low accuracy of young animals for maternal traits (Moore *et al*. 2010). To reflect this, a more realistic proportion of males selected, the top 5% by MI, was also modelled for comparison purposes**.** Bulls selected from the annual PT would be used for one year only and then sold to make way for the selected candidates from the following year's cohort.

In the BLUP and YSG scenarios, where progeny testing was not undertaken prior to sire selection, the best 6 young GEBV and EBV sires (selected on MI at 1.5 years of age) would be used across all nucleus females via AI.

The small numbers of sires selected in these schemes would probably have a negative impact on genetic variation in the nucleus populations. However, given the results of this study, this aspect of nucleus selection was not considered at this stage.

Female. The proportion of females retained for breeding each year within the nucleus group would be subject to certain practical considerations. As described by Bourdon (2000), female selection intensity in beef breeding herds is a balancing act between wishing to retain young females with improved genetic merit in preference to older females in the original nucleus, and having a functional cow herd. For example, not all female selection candidates would; survive to mating, be fertile or be functionally sound. Furthermore, given that first parity females are more prone to

calving difficulty (Eriksson *et al.* 2004), there would probably be an economic cost involved in moving to a (considerably) younger nucleus herd. Considering these factors, the female proportion selected was set at 0.50, reflecting low selection intensity**.** Whilst a more complex rationale could be implemented in calculating this latter figure, it was not relevant to do so, as the selection intensities chosen did not greatly affect this study (see results). This is because, as discussed in Chapter 4**,** the benefit of GS in comparison to conventional (also PT in this case) is independent of selection intensity, when the same selection intensities are applied to genomic and conventional BLUP scenarios.

5.2.8. Generation intervals

PT of bovine males is a lengthy process, and in this study it was considered necessary that males should be selected only after the second calving of their daughters. This was necessary to provide a calving interval performance record for daughters used in the PT. If the candidates were chosen for PT at 1.5 years of age, they would therefore be proven at approximately 6 years of age. Adopting the same methodology as in Chapter 3 (mean parents date of birth to mean offspring date of birth) would give a generation interval of 6 years, which is similar to the timescale involved in dairy PT (Powell *et al.* 2003).

In the BLUP and YSG scenarios, selected bulls could in theory be used for breeding at reproductive maturity (1 to 1.5 years of age). However, in practice they would have to enter AI stations for semen collection, with quarantine periods built in, and then wait until semen was distributed and (9 months later) progeny were born. Given these considerations, a conservative generation interval of 3 years was assumed for these sires.

In all three scenarios, female generation interval was assumed to be 6.2 years, which is the current level observed in the Limousin population (Chapter 3). The

average generation intervals across males and females were therefore 4.6 years for the two young sire schemes and 6.1 for the PT.

5.2.9. Terminal traits

As discussed above, the correlated effect of maternal goal selection on terminal traits was also investigated. The terminal traits included in the MI in this study were the same as those included in the beef TI in Chapter 4, allowing a comparison of terminal gain across the two studies.

5.2.10. Economic Value

The economic value of selection response was estimated using the gene flow methodology described in detail in Chapter 3, with commercial value projected from 10 years of selection in MI over calculated a 20 year timeframe. As per the Amer *et al.* (2007) methodology, the commercial value of genetic gain predicted in nucleus herds was calculated for the 5% of Limousin-sired matings which resulted in females retained for selection in the UK commercial suckler herd.

5.3. Results

5.3.1. Maternal index response and accuracy

When considering MI response with EBV only (scenario 3 in Table 5.2), PT is predicted to outperform the young sire scheme (Scenario 1) by 44% and 65% (0.005 males selected). When including GS with TP = 2000, young sire selection (scenario 2) is predicted to produce a marginally greater response than PT (with no TP), at the cost of lower accuracy. Augmenting TP size from 2000 to 5000, resulted in 28% greater male accuracy in the young sire scenario but only 10% greater male accuracy in PT. Decreasing proportion selected 10 fold (from 0.05 to 0.005) increased response by 36% in scenario 2 (TP = 2000).

Table 5.2 Male selection response and accuracy for Maternal index (MI), in maternal nucleus breeding scenarios, with varied male proportion selected [1,2].

Scenario	Scheme	TP[3] size	Nucleus response (£ / animal /year)		Male Accuracy
			Male proportion selected		
			0.05	0.005	
1	BLUP YS	-	0.91	1.29	0.26
2	Genomic YS	2000	1.22	2.31	0.46
2	Genomic YS	5000	1.54	2.94	0.59
3	PT	-	1.42	2.00	0.53

YS = young sire; PT = progeny testing
[1]Female proportion selected = 0.5 for all scenarios
[2]Female accuracy = 0.25 for all scenarios (no female GS)
[3]TP = genomic training population

5.3.2 Effect on terminal traits

The correlated gain in terminal traits for the young sire scenario, with TP = 2000, was positive, but very low at just £0.03 per animal per year. This compares with the Limousin breed genetic trend in beef TI of about £0.84 per animal per year (from Table 4.3).

5.3.3. Commercial Value

The value of increase in selection response for Scenario 2 over Scenario 1 (for TP = 2000 with 5% of males selected) was only £0.31 per animal p.a. The extra commercial value of this response, using gene flow principles, was projected at £150,000 over 20 years (for the estimated 5.4% of Limousin sired matings resulting in female retained for breeding which sired by NS bulls). A five-fold increase in this value could be achieved with a TP of 5000 animals and 0.005 males selected.

5.4. Discussion

GS, using young sires in a nucleus breeding format, was predicted to offer increased rates of gain in maternal traits, in comparison to active BLUP selection with young sires. Furthermore, these rates of gain were predicted to be similar to those achievable from PT, with reduction in male generation interval offset by a reduced accuracy of selection. However, when considering a realistic TP = 2000 and 5% males selected, the commercial value of response from GS over BLUP from bulls bred in this nucleus was projected to be very low at approximately £7500 p.a. , when averaged over 20 years. This sum is considerably below the likely costs involved in the genotyping requirements for such a scheme. Even when scaled to the entire commercial population, and considering all ‘maternal’ matings, this scheme would be worth less than £1 million over 20 years. Essentially, the number

of commercial matings resulting in a female retained for breeding is too low to in the UK to justify the expense of implementing GS specifically in maternal traits. GS has an element of fixed cost, particularly associated with TP genotyping, which will be difficult to overcome in relatively small populations. Countries with very large beef cow populations, such as the USA or France could perhaps justify this cost, providing breeders (were) engaged in active maternal trait selection. The large (population) scale pedigree beef breeds ,such as US Angus, could also conceivable achieve the larger TP and greater selection intensities, which could considerably increase the merit of GS over conventional BLUP, as demonstrated in Table 5.2.

5.4.1. Effect on terminal traits

This study does suggest that maternal traits could be selected without detrimentally affecting terminal characteristics. This finding is in agreement with an evaluation of long term maternal and terminal trait selection in Limousin cattle in France (Phocas and Sapa, 2004). Therefore, breeders specialising in producing young bulls to breed replacement suckler cows would be able to market these on the basis that they would sire acceptable slaughter progeny also. There are probably limits to this concept in the long term though, particularly in terms of selection for muscling. The Belgian Blue breed is evidence that extreme selection for muscling will (at least) eventually negatively impact key cow traits such as maternal calving ease and fertility (Arthur, 1995).

Breeding for specifically for maternal traits would incur an opportunity cost in not achieving gains in terminal traits. The need to slaughter the male progeny of bulls selected for maternal traits would therefore put these sires at an economic disadvantage compared with those selected for terminal traits.

5.4.2. Maternal Nucleus potential

One UK breed, the Stabilser, has adopted a nucleus breeding concept (Big beef, 2012), with the primary goal of selecting for maternal traits. This herdbook also employs a very high level of performance recording (BASCO, 2012). However, this breed is yet to make a significant impact at a national scale, accounting for less than 1% of beef sires in UK matings (Chapter 2). Terminal selection goals appear to be the priority in most other UK beef breeds Chapter 2).

If terminal selection does not significantly reduce maternal performance, there is little point in selecting specifically for maternal traits if these are not valued by bull buyers. The influence of dairy genes in the suckler herd (Chapter 2) further reduces the need for active maternal trait selection in beef breeds. Probably the most relevant and comprehensive study of this dairy influence was conducted in Ireland (McGee *et al*. 2005; Drennan *et al*. 2006; Drennan and Berry, 2006), a country with similar breed make-up and environmental conditions to the UK. This study found that beef x dairy suckler cows (particularly Limousin x Holstein-Friesian) outperformed beef x beef females in evaluations of the commercial merit of cross-bred suckler cow types. Another less rigorous study in Northern Ireland did not find a superiority of beef x dairy suckler cows, but did conclude that performance of Limousin x Holstein-Friesian suckler cows was similar of the best beef x beef cows (Kirkland and Keady, 2004). If, as indicated by these studies, beef x dairy females which are a by-product of dairy farming (Chapter 2), produce effective suckler cows, at least in comparison to available beef x beef types, the incentive to buy NS bulls with improved maternal genes is greatly diminished. Furthermore, dairy farmers are unlikely to select for maternal traits when buying NS beef bulls as they will mostly sell beef x calves at an early age (Chapter 2 and 3). Even if they (dairy farmers) did wish to select maternal traits, the relevance of for example 200 day maternal weight

(largely a function of milk production) would be questionable when mating to high yielding dairy cows.

Therefore, if the NS bull market dictates that terminal traits continue to be the primary selection focus in commercial suckler herds, selection for maternal traits will only ever exist at a micro level within the major UK beef breeds.

5.5. Conclusion

This exploratory investigation of GS within a nucleus breeding format suggested that while increased rates of genetic gain are possible, projected economic returns from such a scheme do not justify the cost involved. As such, further refinement of the nucleus scheme concept was not considered. The evaluation structure for Terminal GS (Chapter 3) could also produce maternal GEBV in due course, at little extra cost. Therefore, whilst maternal traits are only a minor selection focus of UK pedigree beef breeders, breeders wishing to select for these traits are likely to be able to benefit from the implementation of GS evaluations in terminal traits.

5.6. Appendix.

Table 5.3. Heritability, phenotypic variance and economic weight (which only applies to the five traits which are also profit in the Maternal Value) for traits contributing to the maternal value index.

Recorded trait name[1]	Heritability	Phenotypic Variance	Economic weight (£)
Birth weight-direct, kg	0.23	9.04	-
WT200-direct, kg	0.33	807.45	-
WT200-maternal, kg	0.07	807.45	0.73
WT400, kg	0.40	1589.71	-
Muscle score, score [1]	0.27	1.32	-
Fat Depth, mm	0.29	6394.73	-
Muscle Depth, mm	0.26	2518.42	-
Gestation length-direct, days	0.29	23.81	-
Calving difficulty-direct, score[2]	0.12	1.02	-
Calving difficulty-maternal, score[2]	0.05	1.02	-2.19
Calving interval (CI), (days)	0.09	2367.54	-0.83
Age at first calving, (years)	0.20	0.22	-48.11
Lifespan, parity (days)	0.11	6.06	3.63

[1]Scored 1-15 (higher score = greater muscularity)
[2]Scored 1-5 (higher score = more difficult calving)

Table 5.4. Estimates of genetic correlations between profit traits.

	WT200-maternal	Calving difficulty-maternal	Calving interval	Age at first calving	Life span
WT200-maternal[1]	1	0.37	0	0	0.35
Calving difficulty-maternal	0.37	1	0	0	0.02
Calving interval	0	0	1	-0.32	0
Age at first calving	0	0	-0.32	1	0
Life span	0.35	0.02	0	0	1

[1] WT 200 maternal is sometimes referred to as '200 day milk' in the literature.

Table 5.5 Estimates of genetic (above diagonal) and phenotypic correlation (below diagonal) of recorded traits in the maternal index (MI).

	BWT-direct	**WT200-direct**	**WT200-maternal**	**WT400**	**MSC**	**FD**	**MD**	**GL-direct**	**CD-direct**	**CD-maternal**	**CI**	**AF**	**LS**
BWT-direct	**1**	0.466	-0.106	0.384	0.368	0.092	0.485	0.537	0.566	-0.062	-0.006	-0.006	0.003
WT200-direct	0.270	**1**	-0.119	0.837	0.437	0.210	0.556	0.106	0.291	-0.051	0.007	-0.190	-0.010
WT200-maternal	0.000	0.000	**1**	-0.013	-0.372	0.095	-0.013	0.001	-0.001	0.354	0.001	0.002	0.340
WT400	0.190	0.850	0.000	**1**	0.515	0.119	0.527	0.059	0.111	-0.344	0.007	-0.122	0.002
MSC	0.100	0.480	0.000	0.430	**1**	0.096	0.611	0.189	0.069	-0.097	0.002	0.180	-0.014
FD	0.050	0.170	0.000	0.220	0.160	**1**	0.182	-0.001	0.049	0.002	0.029	-0.001	0.001
MD	0.100	0.320	0.000	0.430	0.490	0.160	**1**	0.191	0.092	0.001	-0.006	0.142	0.005
GL-direct	0.200	0.070	0.000	-0.003	0.120	0.000	-0.007	**1**	0.211	-0.096	0.002	0.002	-0.001
CD-direct	0.310	0.020	0.000	0.030	0.010	0.001	0.001	0.110	**1**	-0.045	-0.205	0.012	0.020
CD-maternal	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1**	0.001	0.001	0.023
CI	0.000	-0.030	0.000	-0.080	0.020	0.030	0.000	0.000	-0.011	0.000	**1**	-0.315	-0.001
AF	0.000	-0.030	0.000	-0.032	-0.003	0.030	0.000	0.000	-0.200	0.000	-0.050	**1**	-0.001
LS	0.000	0.080	0.000	-0.060	0.038	0.000	0.000	0.000	0.000	0.000	0.150	0.060	**1**

[1]Definition of trait name abbreviations: BWT, birth weight; WT200, weight at 200 days; WT400, weight at 400 days; MSC, muscle score; FD, fat depth; MD, muscle depth; GL, gestation length; CD, calving difficulty; CI, calving interval; AF, age first calving; LS, lifespan.

Table 5.6 Performance record information sources for male and female candidates and their relatives in the 3 Maternal Index (MI) nucleus scenarios.

	Male candidate and relative information BLUP and GYS	Male candidate and relative information Progeny Test	Female candidate and relative information (all Scenarios)
Information source	Number of animals recorded		
AFC (PHF)	20	20	3
AFC (MS)	1	5	2
AFC (P)	0	20	1
BWT-direct (C)	1	1	1
BWT-direct (PHF)	5	20	5
BWT-direct (P)	0	20	2
CD-direct (C)	1	1	1
CD-direct (PHF)	5	20	10
CD-direct (P)	0	20	3
CD-maternal (M)	1	1	1
CD-maternal (MS)	1	5	3
CD-maternal (P)	0	20	1
CI (M)	1	1	1
CI (PHF)	5	20	3
CI (P)	0	1	1
FD (C)	1	20	1
FD (PHF)	5	20	2
FD (P)	0	0	2
GL-direct (C)	0	1	1
GL-direct (PHF)	5	20	5
GL-direct (P)	0	20	2
LS (MS)	1	2	1
LS (PHF)	3	5	2
MD (C)	1	1	1
MD (PHF)	10	20	2
MD (P)	0	20	1
MSC (C)	1	1	2
MSC (PHF)	10	20	2
MSC (P)	0	20	1
WT200-direct (C)	1	1	1
WT200-direct (PHF)	10	20	3
WT200-direct (P)	0	20	1
WT200-maternal (M)	1	1	1
WT200-maternal (MS)	5	5	1
WT200-maternal (P)	0	20	1
WT400 (C)	1	1	1
WT400 (PHF)	10	20	3
WT400 (P)	0	20	1

GYS = genomic young sire, PHF = paternal half sibs, MS = mothers sisters, P = progeny, C = candidate, M = mother.

Definition of trait name abbreviations: BWT, birth weight; WT200, weight at 200 days; WT400, weight at 400 days; MSC, muscle score; FD, fat depth; MD, muscle depth; GL, gestation length; CD, calving difficulty; CI, calving interval; AF, age first calving; LS, lifespan.

Chapter 6:

Genomic selection for carcass traits in UK sheep breeding

6.1. Introduction

The UK is the largest sheep meat producer in the EU with a total slaughter value of £1.15 billion in 2010 (AHDB, 2011). Of this, 86% comes from prime lambs slaughtered at less than 1 year of age, which are the breeding goal of the UK sheep industry. In line with this goal, terminal breeds contribute the majority of sires (71%) of, and the greatest proportion of genes (47%) in, the 15 million lambs bred in UK flocks in 2010 (Pollott and Stone, 2006). The Texel breed is the most numerous terminal sire, with 100,000 pure-bred rams (24% of all rams) bred to 3.6 million ewes, mostly cross-bred, in 2003. Whilst the UK sheep population has declined by 13% from the date of the latter survey to 2011 (DEFRA, 2012a), Texel pedigree registrations have increased by 10% over the same period (BTSC, 2012a), suggesting that numbers of Texel rams used in commercial flocks have remained stable or possibly increased. Therefore, the numbers in the Pollott and Stone survey are probably still representative of Texel ram numbers.

Although prime lamb production is the central goal of the UK sheep industry, a substantial proportion of lamb carcasses (42%) fail to meet target grades for conformation and fatness (EBLEX, 2011). Therefore, improvements in carcass traits remain of particular relevance to UK sheep breeding, and using the Texel breed provides a suitable starting point in modelling the potential of genomic selection (GS) to improve these traits in UK sheep breeding.

In chapter 4, it was proposed that commercial phenotypes could be used in genomic evaluation of UK beef breeds, facilitated by the existence of the BCMS database. However, no such recording platform currently exists in UK sheep breeding, with lambs traditionally not required to carry individual identification. Although electronic tagging

(EID) initiatives are underway in UK (Defra, 2012b), these are intended to provide details about the farm of birth, but not as yet any parentage information (such as that recorded in BCMS). The common use of multiple-sire mating, where more than one ram is run simultaneously with a group of ewes during the breeding season, is the major practical barrier in sire identifying of sheep. This breeding method is widely adopted in UK commercial flocks and a large proportion of pedigree flocks (John Vipond, personal communication). Breeders wishing to pedigree record lambs therefore commonly have to verify their parentage, using a DNA test at a cost of approximately £10 per animal. Whilst this expense can be justified by breeders selling pedigree rams for several hundred pounds each, it would represent a prohibitive cost in recording the parentage of commercial lambs which are typically worth less than £100 each. Therefore, it is unlikely that information from commercial progeny of pedigree rams could be collected cost effectively, within the current UK sheep recording structure. This rules out a genomic evaluation based on commercial performance records, such as that hypothesised in Chapter 4. Instead, it appears likely that GS in sheep would have to rely, at least initially, on development of a genomic predictor using phenotypes from pedigree sheep.

A terminal index (TI), comprised of growth and carcass traits, is currently used in UK sheep breeding. The recorded traits in this index are currently assessed by live-weight, ultra-sound scanning and computer tomography (CT). CT of live sheep is a method of accurately assessing the Leanness and fatness of sheep (McFarlane, 2006) and was introduced as a recorded trait in pedigree selection in 2000 (Bunger *et al*. 2011). CT scans currently cost between £60 and £100 per animal and a mobile scanning facility is available in the UK (at the higher cost). Whilst CT phenotypes have a genetic

correlation of 1 with the corresponding carcass profit traits in the TI (see Table 6.6)**,** less than 1% of pedigree registered Texel lambs were CT scanned in 2011 (BASCO, 2012), therefore making CT traits an attractive target for genomic selection (GS).

The aim of this study was therefore to investigate the selection response from the use of GS in carcass traits, when selection candidates would be both genotyped and have CT phenotypes. The economic value of this response will also be estimated to inform as to the commercial viability of implementing GS utilising CT in UK sheep breeding industry. The Texel breed was used as an example UK terminal sire breed in this study, with pedigree and performance records of the national pedigree population obtained from BASCO (2012).

6.2. Materials and methods

6.2.1. Index composition and population parameters

A TI based on the current Texel TI (Signet, 2012) was used as the selection goal in a deterministic simulation to model genetic gain from the inclusion of GBV calculated using CT phenotypes in UK terminal sheep breeding. This index is derived from six selection criterion; eight week weight (8WK), scan weight (SWT), ultrasonic muscle depth (MD), ultrasonic fat depth (FD), CT lean (CT_L) and CT fat (CT_F), and two profit traits weight (LWT) and Fat weight (FWT). The selection traits are currently recorded in live pure-bred pedigree animals, and phenotypic and genetic parameters for these traits were taken from national evaluations of the Texel breed (see Appendix Tables A1 to A4). The economic weights for the profit traits, of £2.66 per kg of LWT and -£1.76 per kg of FWT per lamb born, were adopted from Amer *et al. (*2007), and it was assumed

that these parameters were relevant to pure-breds. Phenotypic information for relatives used in the model was parameterized according to the level of performance recording (for each trait) observed in the UK pedigree Texel population (BASCO, 2012) (see Table 6.7). The mean age of male and female parents of the 2011 Texel lamb cohort, of 2.1 years and 3.4 years respectively (BASCO, 2012), were adopted as generation intervals for this study.

6.2.2. Calculation of the number of independent chromosome segments

This value was calculated as per the description detailed in Chapter 4, with sheep specific parameters adopted from the following sources: The value for effective population (Ne) in Texel sheep, of 305, was taken from Kijas *et al.* (2011), whilst the ovine autosomal length (for the 26 sheep autosomes) of 34.86 Morgans, was calculated by Maddox and Cocket (2007).

6.2.3. Index methodology

A deterministic simulation, using the same model which is described in detail in Chapter 4, was used to predict response and accuracy for TI, when sufficient CT phenotypes of pedigree Texel sheep would be available to create a genomic predictor for selection in the national sheep evaluation. In modelling sheep TI selection, only pure-bred simulations were considered. Therefore, in contrast with Chapter 4, the accuracy of GS in the current study was calculated from the phenotypic performance records of pedigree animals in the TP.

6.2.4. Breeding value convention

In this study, traditional breeding values which are estimated via BLUP and do not include a genomic component will be referred to as EBV. Genomic breeding values, which are calculated from genomic information only, will be referred to as GBV. In the literature, GBV are sometimes referred to as DGV (direct genomic values). The combination of EBV and GBV will be referred to as GEBV, where the breeding value is an index of both traditional and genomic information.

6.2.5. Selection intensity

The initial selection intensity examined in the model was intended to reflect that observed in the current UK pedigree Texel population. The mean TI of males and females selected (sires and dams of lambs born in 2011) in the UK Texel population was equal to the 20^{th} and 55^{th} percentiles respectively of lambs registered in 2011 (BASCO, 2012). Following Falconer and Mackay (1996); if these percentiles are considered to be the mean of a truncated normal distribution of selection candidates 'i', they correspond to a proportion 'p' from which the selected candidates are chosen of 40% of males and 90% of females. These proportions represent selection intensities of 0.966 and 0.195 standard deviation units for males and females respectively.

Typically, 1300 males from the annual cohort (mean over 5 years from 2004 to 2008) became sires in the pedigree Texel population. Therefore, in order to obtain a selection intensity of 0.966, the equivalent of 3250 (1300/0.4) randomly selected males would need to be genotyped per year.

To investigate the effect of increasing male selection intensity on the economic value of GS, intensities of 1.755 and 1.400 s.d. units (reflecting males selected with a mean TI corresponding to the 5^{th} and 10^{th} percentiles respectively, of the breed in 2011) were

also modelled. Genotyping of females was not proposed in this study due to the low selection intensity observed in the existing population.

6.2.6. Training population requirements

Given the low numbers of Texels currently CT scanned (372 males in 2011), it was considered unlikely that an effective TP could be developed from existing animals in the pedigree population. It was therefore proposed that 2000 male selection candidates, among those genotyped, would be CT scanned in the first year of the scheme to create a meaningful genomic predictor. It was assumed that 500 pedigree Texel sheep would be CT scanned in each of the following years of the scheme, which would allow for gradual augmentation of the TP, as well as validation and re-training of the genomic predictor. The numbers of genotypes and CT scans required over the first 10 years of such a scheme are detailed in Table 6.3.

6.2.7. Scenarios modelled

Two scenarios were used to investigate the response from incorporating genomic selection and CT phenotypes in the TI evaluations. In each scenario, genetic gain was calculated for TP sizes of between 500 and 20,000 individuals. GBV was only included in male selection in the model with female selection restricted to conventional pedigree derived EBV only, reflecting the genotyping of male selection candidates only. TI response in both Scenarios was also modelled for current and increased male selection intensities (as described above).

***Scenario 1*, *existing trait selection*.** This scenario modelled selection for the TI with the existing level of phenotype recording observed in the population (see Table 6.7). The six recorded traits; eight week weight (8WK), scan weight (SWT), ultrasonic muscle depth (MD), ultrasonic fat depth, CT lean (CT_L) and CT_F (CT_F) were first evaluated with EBV only at TP = 0 (i.e. no genomics). The impact of combining EBV with genomic information (GBV) to produce GEBV was then modelled for the two weight and two ultrasound traits. Thus GEBV was modelled without genomic information for the two CT traits.

***Scenario 2, CT phenotypes*.** This scenario initially modelled the use of a genomic predictor developed from a TP comprised of pedigree animals with phenotypic CT records and genotype information. Therefore, in this case, the TI included GEBV information from all six recorded traits.

GBV only: The potential of selection with genomic information only, without any phenotypic recording outside the TP, was investigated by predicting male TI accuracy when GBV alone (derived with TP =2000) was available for; 1) the two 2 CT traits and 2) all 6 recorded traits.

CT EBV: Response was also predicted when all male selection candidates would be CT scanned and no GS took place.

6.2.8. Dissemination of genetic gain to the commercial population. In order to estimate the commercial value of genetic improvement simulated in the elite population, the method described in detail by Amer *et al.* (2007), and used previously in Chapter 4, which is based on discounted gene flow principles was adopted. Genetic gains for the two profit traits, calculated in the 3 scenarios, were used as inputs for this model. Elite

population gains were thus translated into estimates of financial benefit to the commercial industry using the principle of discounted genetic expressions. However, in contrast to Chapter 4 and in accordance with the knowledge that commercial phenotypes are unlikely to be readily available for sheep GS, no account was taken of genotype by environment interaction in this study (see Discussion).

Commercial industry parameters for the model were taken from Pollott and Stone (2006). This survey estimated that 100,000 Texel rams were mated to 3.5 million commercial ewes each year in the UK, suggesting that 33,000 replacement rams would be required each year assuming ram working life of 3 years breeding (SAC, 2008). With approximately 33,000 Texel males registered per year in pedigree flocks (BTSS, 2012), and around 1300 retained for pedigree breeding p.a., it appears that almost all the commercial sector needs for breeding males can be met by rams born in pedigree flocks. Therefore it was assumed in this study that all terminal Texel genes in commercial lambs originated within 1 generation from pedigree flocks.

In 2011, 94% of registered lambs were attributed EBV in breed genetic evaluations. This figure was adopted in this study, as the proportion of Texel rams which would disseminate gains from GS in the pedigree population to commercial flocks.

Proportion of Terminal matings: In order to calculate the proportion of Texel-sired matings which resulted in prime slaughter lambs p.a. it was necessary to estimate the numbers of matings which result in a female retained for breeding in commercial flocks. Pollott and Stone (2006) detail that there were 1,444,500 Texel sired ewes in pure- and cross-bred flocks. Assuming that 100,000 of these ewes are registered in the Texel flockbook, the remaining 1,344,500 are commercial ewes which have been retained as (Texel-sired) replacement females. Considering a mean ewe productive life of longevity of 5 years (i.e. 5 lambings) (SAC, 2008), 20% of this total (1,344,500 x 0.2 = 269,000)

are typically retained from Texel matings each year as replacement females. If the 3.5 million commercial ewes mated to Texel rams p.a., rearing 1.5 Lambs per ewe p.a. (SAC, 2008), 5.25 million Texel-sired lambs would be reared each year. Therefore an estimated 5% (269,000 out of 5,250,000) of Texel lambs are retained as replacements p.a., and thus 95% of Texel-sired matings result in prime slaughtered progeny p.a. this proportion was considered in assessing the commercial value of TI gain in this study.

Number of commercial ewes mated with improved rams: Out of the 3.5 million commercial ewes are mated annually to Texel rams, it was assumed that 94% (proportion of Texel lambs with EBV available) of 95% (proportion of terminal matings), i.e. 89% (3.115 million ewes), would be mated to improved Texel rams, with the objective of producing prime slaughter progeny.

A discounting rate of 3.5% (HM treasury, 2012) was used in calculating the net present values associated with the genetic gain modelled from GS. The model accounts for the long term nature of selection by calculating cumulative returns over a 20 year period from an initial 10 years of genetic improvement. In the case of this study, this represents the returns from 10 years of funding selection using genomic information. Breakeven genotyping costs were calculated for the 2 scenarios and variations of male selection intensity.

6.3. Results

6.3.1. Male terminal index Accuracy

GS using a genomic predictor calculated from a TP, with 2000 genotyped animals with CT phenotypes (Scenario 2 in Table 6.1), is predicted to increase male selection accuracy by 0.133, resulting in 55% greater genetic gain over conventional BLUP selection (TP =0). With TP = 5000, male accuracy increased 0.23, resulting in 94% greater genetic gain. In contrast, when the genomic predictor was to be calculated using only weight and ultrasound traits (Scenario 1 in Table 6.1), and without CT phenotypes, male accuracy increased by only 0.026 for TP = 2000 and 0.047 for TP = 5000. Figure 6.1 illustrates the increasing superiority of male selection accuracy for Scenario 2 over Scenario 1, with larger TP size. Female accuracy was similar to male at 0.240, with conventional BLUP only, and constant in both Scenarios and their TP variations as genotyping of females was not modelled.

Table 6.1 Terminal index accuracy in male selection.

Scenario	1*	2**
TP		
0***	0.244	0.244
350	0.252	0.279
500	0.255	0.291
1000	0.260	0.325
2000	0.270	0.377
5000	0.291	0.474
10000	0.310	0.562
20000	0.332	0.647

*Scenario 1 modelled GEBV for the four weight and ultrasound recorded traits only (eight week weight, scan weight, ultrasonic muscle depth and ultrasonic fat depth) and no computer tomography phenotypes.
**Scenario 2 modelled GEBV for all six recorded traits, including the two computer tomography traits (CT lean and CT fat).
***TP = 0 represents conventional BLUP selection without computer tomography phenotypes.

If the existing number of pedigree Texels with CT scans (approximately 350 animals annually) were used as the TP in Scenario 2, the predicted accuracy would be 0.279, which was than 0.035 greater than with TP = 0, but 0.098 less than using a TP = 2000, which would take six years to achieve with the existing rate of CT scanning. Obtaining CT phenotypes for all male selection candidates was predicted to result in accuracy ,with a TI comprised of traits with EBV only, of 0.741, which was greater than predicted GEBV accuracy with TP = 20,000 (Table 6.1).

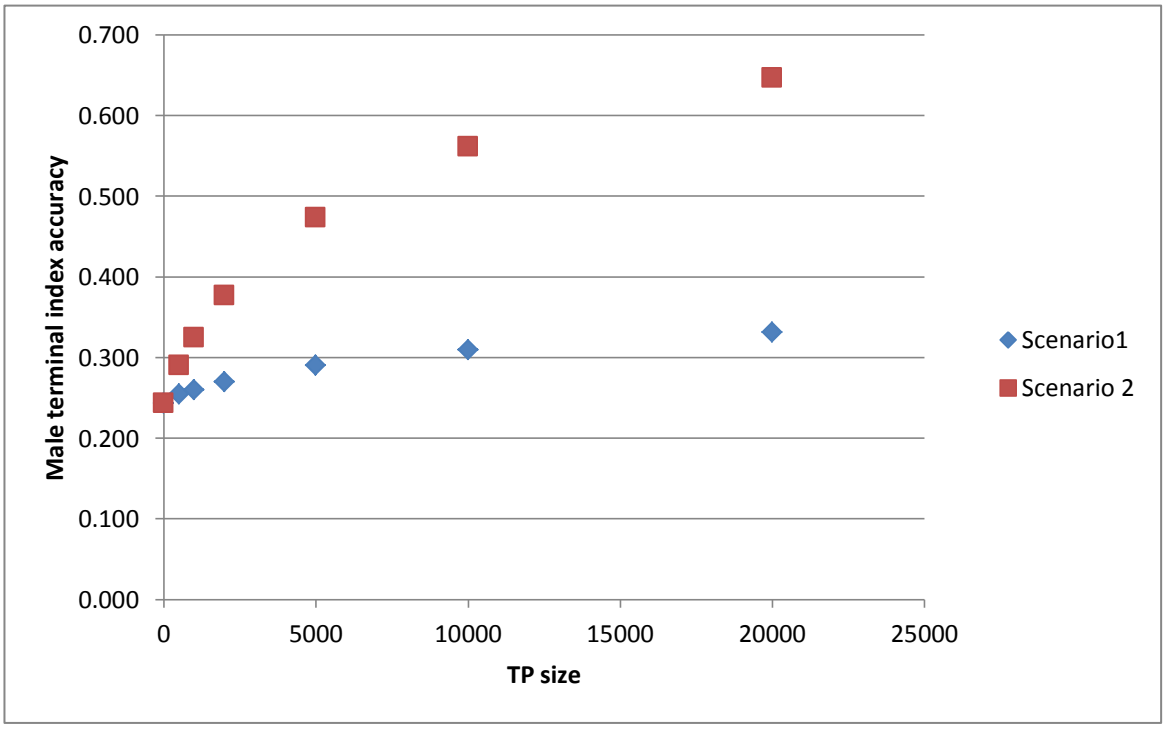

Figure 6.1. Male terminal index accuracy for Scenarios 1 and 2 with varying genomic training population sizes.
Scenario 1 modelled GEBV for the four weight and ultrasound recorded traits only (eight week weight, scan weight, ultrasonic muscle depth and ultrasonic fat depth) and no computer tomography phenotypes.
Scenario 2 modelled GEBV for all six recorded traits, including the two computer tomography traits (CT lean and CT fat).
TP = 0 represents conventional BLUP selection without computer tomography phenotypes.

6.3.2. GBV only

When the TI was modelled with only GBV information from the two CT traits (and no EBV information), an accuracy of 0.30 was predicted (with TP = 2000), which is similar to Scenario 1 with TP = 10,000 and Scenario 2 for TP = 500. With GBV only for all six traits, the TI accuracy predicted was only marginally greater at 0.33.

6.3.3. Terminal index response

Figure 6.2 shows total (male plus female) response to TI selection, when the proportion of male and female candidates selected was 0.4 and 0.9 respectively. These proportions selected correspond to the selection intensity for TI currently observed in the UK pedigree Texel population.

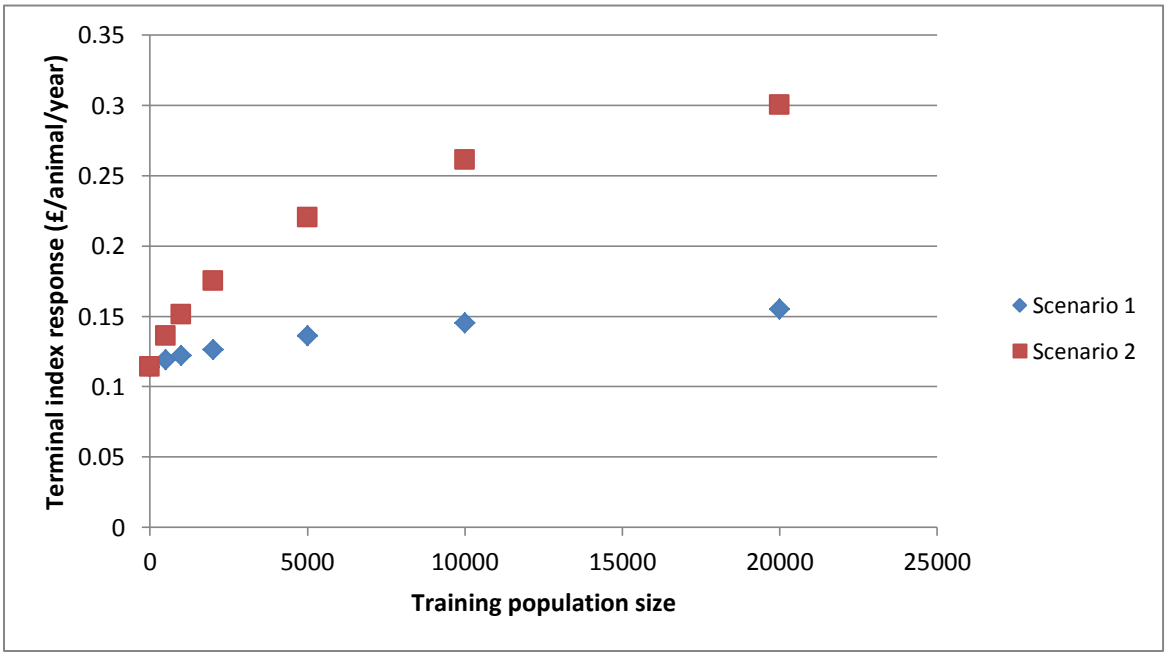

Figure 6.2 Terminal index response (£ per animal per year), (male plus female), for scenarios 1 and 2 with varying genomic training population sizes. Proportion of male selected = 0.4).

As female response was negligible (£ 0.023 /animal/year) in both scenarios, the pattern of genetic gain with increasing TP size closely resembles that of male accuracy in Figure 6.1.

When an increase in male selection intensity was modelled (Table 6.2), an approximately proportional, as female response was constant, increase was observed in total TI response. Increasing male selection intensity improved the economic value of both GS and conventional BLUP selection (Table 6.3). Furthermore the net gain from GS over current BLUP selection also increased. However, due to the increased number of selection candidates and associated increased genotyping costs, breakeven genotyping cost reduced as male selection intensity increased.

Table 6.2 Terminal index response (male plus female) in Scenario 2* with varying training population sizes and male selection.

TP size	Proportion of the annual cohort from which males are selected per year	Male selection intensity (s.d. units)	Terminal index response (£/animal/year)
0	0.1	1.755	0.21
	0.2	1.400	0.17
	0.4	0.966	0.11
2000	0.1	1.755	0.32
	0.2	1.400	0.25
	0.4	0.966	0.18
5000	0.1	1.755	0.40
	0.2	1.400	0.32
	0.4	0.966	0.22

*Scenario 2 modelled GEBV for all six recorded traits, including the two computer tomography traits (CT lean and CT fat).
TP = 0 represents conventional BLUP selection without computer tomography phenotypes.

Table 6.3 Projected gain and breakeven genotyping costs, resulting from 10 years of genomic selection in Scenario 2*, with 10 years of investment returns measured over 20 years.

Training population size	Male selection intensity (s.d. units)	Number of male selection candidates per year	Number of genotypes required over 10 years[1]	Number of CT** scans required over 10 years[2]	Total cost of CT** scanning over 10 years at £100 per animal (£)	Economic value of male selection response (£ million)	Gain from genomic selection[3] (£ million)	Breakeven genotyping cost per animal[4] (£)
	1.755	13 000	-	-	-	22.33	-	-
0	1.400	6 500	-	-	-	18.58	-	-
	0.966	3 250	-	-	-	12.88	-	-
	1.755	13 000	130 000	6 500	650 000	35.08	12.75	95
2000	1.400	6 500	65 000	6 500	650 000	28.58	10.00	148
	0.966	3 250	32 500	6 500	650 000	19.90	7.02	196
	1.755	13 000	130 000	9 500	950 000	44.54	22.21	171
5000	1.400	6 500	65 000	9 500	950 000	36.31	17.73	273
	0.966	3 250	34 250	9 500	950 000	25.03	12.15	327

*Scenario 2 modeled GEBV for all six recorded traits, including the two computer tomography traits (CT lean and CT fat).
**CT = computer tomography

[1]The number of genotypes required over 10 years of investment was calculated from the number of male selection candidates per year x 10, plus the training population size. In the case of TP = 5000, an additional 1750 genotypes are required in year 1.
[2]The number of CT scans required over 10 years is equal to the number of animals in the training population plus 500 p.a. over the following 9 years. E.g. for TP = 2000, the number of scans required = 2000 + (500 x 9) = 6500.
[3]Gain from genomic selection was calculated as the economic value of male selection response minus, for each variation of TP size (2000 and 5000) and male selection intensity, minus the value of conventional BLUP selection, for corresponding variations of male selection intensity. E.g. for a TP = 2000, with male selection intensity of 0.966, the benefit of GS was £19.90 million minus £12.88 million, giving £7.02 million.
[4]The breakeven cost of genotyping is the gain from genomic selection, minus the cost of 10 years of CT scans, divided by the number of genotypes required. E.g. for TP = 2000, with male selection intensity of 0.966, breakeven genotyping cost is £7.02 million minus £650,000 and then divided by 32,500, giving £196 per animal (assuming 1 genotype per animal).

6.4. Discussion

This Chapter investigated the potential genetic and economic benefits of implementing GS with CT phenotypes in UK terminal sire sheep breeding. The Texel, which is the sire breed of approximately one quarter of lambs born in the UK each year (Pollott and Stone, 2006), was used as an example terminal sire breed in this study**.** CT scanning provides valuable phenotypes in terminal sheep selection, and has a well established infrastructure the UK, with both static and mobile scanning facilities (Bunger *et al*. 2011). However, uptake of these facilities is low, with for example, only 350 pedigree Texel lambs scanned in a typical year (1% of the male cohort). Furthermore, only 4% of the 2011 male cohort had sires which had been CT scanned. The advent of GS has created an opportunity for CT to make a considerably greater impact on UK terminal sheep breeding. This study predicts that a TP of 2000 Texel selection candidates with genotypes and CT scan could result in approximately 50% greater genetic gain for TI, in comparison with BLUP selection without CT phenotypes. The economic value of this gain does depend on a number of important assumptions which will be further explored in this Discussion. Given that the breakeven genotyping costs for this scheme are projected to be only marginally in excess of current marker panel costs, variation around these assumptions would be critical to the financial viability of the scheme proposed in this study.

6.4.1. Narrow selection goal

In comparison to the beef TI modelled in Chapter 4, the sheep index used in this study could be considered a narrow selection goal. No ease of birth trait is included in the current Texel TI (Signet, 2012), and accordingly, in order to reflect existing selection,

lambing ease, which is a recorded trait in pedigree Texels, was not included in the TI used in this study. Given the negative correlation between lambing ease and lean growth traits in Texel (e.g. -0.11 with 8 week weight and -0.21 with ultrasonic muscle depth) deterioration in this trait would be expected by exclusion of lambing ease in the TI. Narrow selection goals, such as that modelled in this study, therefore tend to be unsustainable in the long term, due to undesirable effects on negatively correlated traits such as lambing ease, as evidenced for example by the study of Rauw et al. (1998). Selection using the existing Texel TI therefore requires long-term monitoring and may eventually need to include lambing ease as a component trait.

6.4.2. Selection for leanness

The current UK Texel evaluations use an ATAN statistical function (Signet, 2012), which decreases the economic value of fat depth reductions within the Texel TI of animals with extreme negative fat depth EBV. The goal of this index modification is to promote a moderate reduction in genetic merit for carcass fat, whilst avoiding selection for extreme leanness in sheep. This transformation was not included in the model used in this study. A decrease in fat depth of -0.018 mm per animal per year was predicted with GS for TP = 2000 in Scenario 2 (this is a TI component trait result not presented previously). This compares with the breed genetic trend of -0.009 mm (mean over 10 years up to 2012). However, the difference between these figures represents an increase of only 0.3% in the mean fat depth which was 3mm (phenotypic) for lambs born in 2011. The results predicted in this study therefore do not rely on an extreme or undesirable decrease in fat depth to achieve TI gains.

6.4.3. Dissemination of improved genes and uptake of genetic technology

This study used an optimistic estimate of the rate of dissemination (89%) of improved genes to the commercial population in order to estimate the maximum economic benefit achievable in commercial flocks from GS implementation in the Texel breed. In contrast, Amer *et al*. (2007) adopted a considerably more conservative figure of 30% (termed penetration rate in that paper) across all terminal sire sheep breeds. This value of 30% was based on the amount of performance recording observed in pedigree breeds, rather than the proportion of the breed being attributed EBV, which was the method used in the current study. As described earlier in the Chapter, this study has taken the approach that if a breeding value can be estimated for a non-performance recorded animal, then the accuracy of that estimation will be improved with GS. However, this would only lead to greater genetic gain if the animal is subsequently selected on the basis of GEBV. The Amer *et al*. (2007) dissemination rate does not account for genetic progress being made in flocks that do select on the basis of EBV, but that do not undertake phenotypic recording. Most importantly, this lower dissemination rate also implies that the performance recorded flocks do not constitute an elite breeding core from which genes are disseminated widely to other pedigree flocks, which would be in contrast to the findings in Chapter 3 for Limousin cattle. Two aspects of Texel selection shed light on the likely influence of recorded flocks;

1) The proportion of Texel lambs born in 2011, with performance recorded sires for a growth trait (24%) is considerably lower than that observed for Limousin calves (50%) in Chapter 3. If recorded flocks are at the top of the breeding pyramid, the speed of dissemination of genes from recorded flocks to the commercial population will be slower than observed in the Limousin population.

2) Whilst rams with greater selection indices, among those performance recorded, are publicised as achieving higher prices than lower indexed ones at national pedigree auctions (e.g. BTSS, 2012b), analysis of the same sales reveals that performance recorded rams achieve lower average sale prices than their more numerous non-performance recorded counterparts (Non-performance recorded rams do not have EBV published in Texel sale catalogues). This suggests that performance recorded rams are less valued than rams chosen on visual assessment only and is therefore strong evidence that these rams do not come from the top of the breeding pyramid.

These observations suggest that the current dissemination rate in the Texel population may be closer to that used by Amer *et al*. (2007) than the rate adopted in the current study. Breakeven genotyping costs could therefore be as low as two thirds of the values predicted in Table 6.3. For example with TP = 2000 and at current selection intensity, the breakeven cost for a 30% dissemination rate would be £65 rather than the £196 projected for the 89% rate.

The economic value of gains predicted from GS in this Chapter, with even the lowest selection intensity scenario, thus likely represent a best case scenario with significant possible downside.

6.4.4. Cost of existing performance recording

It was predicted that similar accuracy could be obtained from GBV alone, using a TP with CT phenotypes, to that currently possible with EBV with the current level of performance recording for non-CT traits. Amer *et al*. (2007) suggested that existing

performance recording cost £8.50 in Signet membership per ewe to breeders, for assessment of weight and ultrasound traits only. Estimating that the 16,500 Texel lambs recorded annually have around 12,000 dams, would imply that approximately £100,000 is spent on conventional recording p.a., without taking into account the breeders own labour costs associated with weighing and ultrasound scanning. This cost is similar to the projected annual cost for the 2000 TP scenario at existing selection intensity in Table 6.3, assuming genotyping to cost £100 per animal. Thus, from a financial perspective, one option could be to cease performance recording of non-CT traits in pedigree sheep, and concentrate resources solely on developing a genomic TP and genotyping of selection candidates. This potential cost saving was not included in the calculation in this study, as it is unlikely to be a strategy implemented until the merits of GS are proven in sheep breeding.

6.4.5. Genotyping options

The breakeven genotyping costs projected were highly sensitive to the number of selection candidates proposed. In breed-wide schemes such as this, where selection decisions are made by thousands of individual breeders, it is not possible to definitively predict the numbers of selection candidates considered. This study therefore adopted an estimate based on the selection intensity modelled, to give an indication of the likely numbers involved. Paradoxically this method resulted in less favourable predicted breakeven genotyping costs with increasing selection intensity (and thus greater numbers of selection candidates). Henryon *et al.* (2013) addressed the issue of genotyping large numbers of selection candidates, proposing the use of pre-selection on EBV information, prior to genotyping. This paper estimated that, when the genomic prediction reliability was 0.1 (corresponding to the accuracy predicted in the current

study for TP of between 1000 and 2000 animals), genotyping only 5% of candidates could achieve 86% of the genetic gain attainable with genotyping 100% of candidates. Thus considerably more favourable breakeven genotyping costs may be achievable than those predicted in the current study.

Genotype imputation is another option to reduce selection candidate genotyping costs (Habier *et al*., 2009). This technique uses low density genotyping panels to predict (or impute) the genotype of individuals in the population from high density genotypes of their ancestors or siblings. The method therefore relies on genetic LD within (e.g. sires and their progeny) and between families, to allow the genotypes of a dense group of SNP to be predicted from a comparatively sparse set of markers. Hayes *et al.* (2012) demonstrated that genotyping sheep with 5K marker panels could accurately predict between 70 and 80% of the SNP genotypes obtained with 50K genotyping panels. Whilst some of this accuracy may be attributable to chance, due to low minor allele frequency, similar positive results from imputation have been obtained when using correlation as a measure of accuracy, which eliminates the minor allele frequency issue problem (e.g. Huang *et al*. 2012). An option could be to genotype male selection candidates at low density and then re-genotype (some or all) candidates which are selected as sires in the pedigree population.

As the genotyping of selection candidates was predicted to be by far the largest cost associated with the schemes described in this study, the removal of the need to genotype all candidates and the use of imputation could favourably and significantly increase breakeven genotyping costs.

6.4.6. Multi-breed genomic selection

The two other major sire breeds in the UK (Suffolk and Charollais) have a combined share of the terminal sire market which is approximately similar to that of the Texel (Pollott and Stone, 2006). Cost savings may be achieved if these breeds could be evaluated alongside Texel in multi-breed GS. However, there is as yet no evidence of multi-breed genomic prediction being effective. For example, Daetwyler et al. (2012) reported GBV accuracy of up to 0.31 in carcass traits recorded at slaughter, when using a genomic predictor calculated with multi-breed TP of substantial sizes of up to 8000 animals (depending on the trait). These accuracies were significantly lower than those predicted within-breed for Scenario 2, with TP sizes of 5000 and above, in the current study. Indeed, Daetwyler *et al*. (2012) concluded that 'across-breed' prediction was limited with the 50K genotyping panel. Worthwhile multi-breed prediction therefore remains an unproven hypothesis in livestock breeding.

6.5. Conclusion

This study predicted that GS using CT phenotypes could offer increased rates of genetic gain for terminal trait selection in sheep, in comparison with either BLUP selection or GS, without CT phenotypes. Breakeven genotyping costs were predicted to be marginally in excess of current genotyping costs, when adopting an optimistic rate of dissemination of improved genes. These costs could be significantly reduced by the use of imputation and pre-selection of candidates (for genotyping) based on EBV. Nevertheless, the economic viability of this scheme is much more sensitive to the assumptions adopted in this study than was the case for the beef GS scheme suggested in Chapter 4. Implementation of GS at a breed-wide level in the sheep sector is therefore considered to involve a greater element of risk than in beef.

It could be argued that investment in sheep genetic improvement would be better spent incentivising the uptake of existing EBV technology, whilst awaiting developments in GS which make this concept more viable in sheep breeding. For example, greater adoption of CT recording among selection candidates, and evaluation via EBV only, would result in gains comparable to those predicted with GS using large TP sizes.

However, in the longer term, GS does offer the possibility of replacing the existing performance recording structure. Future reductions in genotyping costs could bring this prospect sharply into focus.

6.6 Appendix 1.

Table 6.4 Heritability, phenotypic variance and economic weight of recorded and goal traits in the terminal index

Trait name[1]	Heritability	Phenotypic Variance	Economic weight (£)
8WK[1], kg	0.25	13.05	-
SWT[1], kg	0.41	31.01	-
MD[1], mm	0.29	7.12	-
FD[1], mm	0.37	1.06	-
CT_L[1], kg	0.43	2.49	-
CT_F[1], kg	0.32	1.92	-
LWT[2], kg	0.28	3.31	2.66
FWT[2], kg	0.29	4.84	-1.76

Definition of trait name abbreviations of existing TI traits:
[1]Recorded traits; 8WK, eight week weight; SWT, scan weight; MD, ultrasonic muscle depth; FD, ultrasonic fat depth; (CT_L) computer tomography lean and (CT_F) computer tomography fat.
[2]Goal traits; LWT, lean weight; FWT, fat weight.

Table 6.5 Estimates of genetic (above diagonal) and phenotypic (below diagonal) correlations between recorded traits in the terminal index

	8WK	SWT	MD	FD	CT_L	CT_F
8WK	1.00	0.90	0.49	0.36	0.82	0.67
SWT	0.73	1.00	0.47	0.37	0.83	0.68
MD	0.40	0.56	1.00	0.24	0.41	0.23
FD	0.31	0.27	0.33	1.00	-0.06	0.55
CT_L	0.66	0.85	0.53	0.25	1.00	0.38
CT_F	0.54	0.72	0.38	0.53	0.38	1.00

[1]Definition of trait name abbreviations of existing TI traits : 8WK, eight week weight; SWT, scan weight; MD, ultrasonic muscle depth; FD, ultrasonic fat depth; Computer tomography lean (CT_L) and Computer tomography Fat (CT_F).

Table 6.6 Estimates of genetic correlations between recorded traits and goal traits (first 6 columns), and genetic correlations between goal traits (last 2 columns), in the terminal index

	8WK[1]	SWT[1]	MD[1]	FD[1]	CT_L[1]	CT_F[1]	LWT[2]	FWT[2]
LWT[2]	0.82	0.67	0.23	0.55	1.00	0.38	1.00	0.38
FWT[2]	0.54	0.72	0.38	0.53	0.38	1.00	0.38	1.00

Definition of trait name abbreviations of existing TI traits:
[1]Recorded traits; 8WK, eight week weight; SWT, scan weight; MD, ultrasonic muscle depth; FD, ultrasonic fat depth; Computer tomography lean (CT_L) and Computer tomography fat (CT_F).
[2]Goal traits; LWT, lean weight; FWT, fat weight.

Table 6.7 Relative performance record information sources used for TI simulation (estimated from BASCO, 2012)

Information source name[1]	Number of animal records (Male)	Number of animal records (Female)	Number of animal[2] records (Progeny Test)
8WK (candidate)	1	1	1
SWT (candidate)	1	1	1
MD (candidate)	1	1	1
FD (candidate)	1	1	1
CT_L (candidate)	0	0	0
CT_F (candidate)	0	0	0
8WK (parental half-sib)	5	5	10
SWT (parental half-sib)	5	5	10
MD (parental half-sib)	5	5	10
FD (parental half-sib)	5	5	10
CT_L (parental half-sib)	0	0	0
CT_F (parental half-sib)	0	0	0
CT_M (parental half-sib)	0	0	0
8WK (progeny)	6	0	20
SWT (pogeny)	6	0	20
MD (pogeny)	6	0	20
FD (pogeny)	6	0	20
CT_L (pogeny)	0	0	20
CT_F (pogeny)	0	0	20

[1]Definition of trait name abbreviations of existing TI traits; 8WK, eight week weight; SWT, scan weight; MD, ultrasonic muscle depth; FD, ultrasonic fat depth; Computer tomography lean (CT_L) and Computer tomography fat (CT_F).

[2]Progeny test also simulated with 5 progeny

Chapter 7:

General Discussion

7.1 Great expectations

Many animal scientists expect(ed) the impact of genomic selection in animal breeding to be fundamental. This sense of potential was aptly conveyed by Dekkers (2009) when suggesting that GS was 'expected to lead to a paradigm shift in the design and implementation of livestock breeding programmes'. Goddard and Hayes (2009) further proposed that GS would 'double the rate of genetic improvement per year in many livestock systems'. The strong uptake of semen from young genomic sires suggests that these great expectations are being realised in dairy cattle breeding. Hayes *et al*. (2009) observed that GS was 'revolutionizing dairy cattle breeding', whilst Wiggans *et al*. (2010) suggests that 'implementation of genomic evaluation has caused profound changes in dairy cattle breeding'.

Given the success in dairy selection, beef and sheep breeding research has begun to focus on the potential for GS in these sectors. As discussed at length in the Introduction, the potential for GS in these sectors is less immediately apparent than in dairy. Attention has especially turned to the possibilities for GS to be used in breeding traits which are difficult to measure, largely due to cost and practicality issues, in beef and sheep selection candidates. These include: carcass traits (Van der Werf 2009; Dekkers, 2010; Van Eenennaam *et al.* 2011), maternal traits (Van der Werf 2009, Van Eenennaam and Drake, 2012), feed efficiency (Sawalha *et al.* 2010; Van Eenennaam and Drake, 2012) and disease (Dekkers, 2010; Van Eenennaam and Drake, 2012).

This thesis sought to explore whether GS expectations can also be fulfilled in beef and sheep breeding sectors in the UK.

7.2 Thesis summary

In attempting to answer the above question, this study first concentrated on the potential of genomics in UK beef and then sought to apply lessons to the sheep sector. The first step was to profile the beef breeding structure to provide key facts for use in modelling the potential genetic and economic impacts of GS. Unlike the commercial sheep breeding sector which has been repeatedly surveyed, most recently by Pollott and Stone (2006), detailed information was lacking about the breed makeup of the commercial beef herd in the UK prior to this Thesis. In Chapter 2 it was found that 88% of beef-sired matings resulted in prime slaughter progeny, with only 12% (7% excluding dairy cross-breds) resulting in a female retained for breeding. Almost all commercial cattle matings involved cross-breeding. The continuing strong influence of dairy genes in the beef breeding sector was also confirmed, with Holstein-Friesian contributing 28% of suckler cow genes. Pure-bred NS sires, mainly pedigree registered, were identified as the likely originators of most genes in an almost entirely cross-bred commercial beef population. Correlations between sale prices of these bulls and their TI values suggested a moderate uptake of EBV technology in UK beef breeding.

In Chapter 3 the pedigree breeding structure of the most influential UK beef breed, the Limousin, was examined. Selection intensity for terminal traits and generation interval were quantified for use in Chapter 3. From a profile of herd influence, it was clear that a small group of Elite breeders drive selection within the breed. Uptake of phenotypic performance recording is strong within this core group. The UK Limousin breed continues to be heavily influenced by imported French genes. Importantly, this structure of this breed suggested that genetic gains in elite herds were quickly and widely disseminated to the commercial population.

Using parameters form Chapters 2 and 3, genetic gain was predicted for GS in terminal beef traits. Little advantage over current BLUP selection was predicted for phenotypes already recorded. Selection for novel carcass traits facilitated by GS, and accounting for likely G x E interaction, was projected to offer substantial increases in genetic gain (40 to 66%) when considering feasible TP sizes 2000 to 5000 individuals. At this stage no major structural change was modelled, except for the inclusion of routinely recorded abattoir carcass phenotypes in pedigree evaluations. The merit of GS was thus considered when being 'overlaid' onto the existing UK beef breeding structure, with identical selection intensity and generation intervals to those currently observed in a typical pedigree beef population. Increased response predicted as a result of GS was therefore due to greater accuracy alone.

In contrast, it was necessary to consider structural change in Chapter 5, when assessing the potential for GS in maternal beef traits, given that no objective evidence of selection (using BLUP) exists in UK maternal breeding. GS was predicted to offer increased gain over active BLUP selection within a nucleus breeding format. However, the low replacement rate of commercial females identified in Chapter 2, limited the number of genes per year which could be improved through GS and there was thus little financial benefit predicted.

Given the lessons from the beef Chapters, together with evidence from Pollott and Stone (2006), CT trait selection in the most numerous terminal sire breed (the Texel) was considered as a promising starter point for GS in UK sheep breeding in Chapter 5. The low uptake of CT technology in the UK afforded these traits similar properties to the novel carcass phenotypes modelled in Chapter 4, in that they had considerably stronger correlations to selection goals than conventional ultrasound and weight phenotypes.

Accounting for G X E was not considered in this Chapter, due to the absence of parentage recording in commercial flocks. Whilst a substantial percentage improvement in TI gain was predicted, breakeven genotyping costs were less favourable than estimates for beef breeding in Chapter 4.

7.2.1. Footnotes; two factors affecting rate of genetic gain

In this thesis, artificial insemination (AI) was not proposed as a tool to disseminate genetic gain more rapidly and thus increase the likelihood of GS adoption in beef and sheep sectors. Equally the Bulmer effect was not incorporated in the selection index model used in Chapters 4 to 6. The reasons for non-inclusion of these two topics will now be briefly considered.

7.2.1.1. Artificial insemination

There is virtually no AI in commercial beef (suckler) and sheep breeding in the UK (OFT, 2004; Amer, 2007). The main reason for this is likely to be that AI does not offer an economic advantage in semi-extensive breeding herds and flocks (Todd, 2007). For example, the current difference in TI between breed-average and top 1% bulls is £20 for 2011 Limousin bulls (BASCO) and £33 for 2011 Charolais bulls (ABRI). Therefore, the extra economic value of gain from using a top 1% sire via AI compared with using a breed average sire by NS, is unlikely to provide extra return after accounting for the costs of synchronising oestrus and insemination, and particularly labour involved in these procedures (Todd, 2007). Therefore, breeding companies currently only play a limited role in UK suckler beef and sheep sectors. In the future, improvements in fecundity of sexed semen may make AI more viable in commercial beef and sheep breeding. The ability to produce largely male progeny would be a substantial economic

advantage in UK commercial beef and sheep systems. The improvement of sexed semen technology could therefore be a driver for increased breeding company influence in these sectors, which would open up greater possibilities for GS. Until then it appears likely that breed organisations such as herdbooks will be the first entities to implement GS in beef and sheep, and do so at a breed-wide level, rather than private companies such as in pig and poultry breeding with segregated nucleus populations.

7.2.1.2. The Bulmer effect

Truncation selection, where the best parents are selected each generation for a given (polygenic) trait, is associated with the temporary loss of genetic variation in the population under selection (Bulmer, 1971). Genetic gain is directly proportional to the genetic standard deviation, as described by the 'breeders' equation' (Lush, 1937) and is therefore related to the amount of genetic variance in the population. This thesis judged the value of GS by comparing response with that achievable from conventional BLUP selection and adopted the selection intensity currently observed in Limousin and Texel populations, in the main comparative scenarios. The Bulmer effect was not taken into account in this analysis. Dekkers (1992) suggested that the Bulmer effect would be similar across breeding schemes which adopted the same selection intensities, irrespective of selection accuracy and trait heritability. According to the Dekkers study, asymptotic response for both BLUP and GS, with 20 to 40% of males selected and 100% of females would be in the order of 10 to 15% lower than the gains predicted in Chapters 4 and 6 in absolute terms. With specific reference to GS, Van Grevenhof *et al.* (2012) suggest that the scale of the Bulmer effect with this (GS) concept would be similar to that observed for BLUP selection. Bijma, 2012 argues that the *relative* benefit of GS (in comparison with BLUP) may be underestimated due to overestimation of

parent average accuracy by BLUP with truncation selection. From the evidence of these studies, not incorporating the Bulmer effect in simulations in this thesis, will not have overestimated the relative merit of GS in comparison with BLUP.

The remainder of the general discussion will concentrate on three topics;

1) Drivers of uptake of new genetic technologies and a consideration of potential for GS in traits not previously considered in this thesis.
2) Future possibilities of GS; International cooperation in TP development and multi-breed selection.
3) The end of pedigree? ; Consequences for genetic diversity.

7.3. Drivers for uptake of genomic selection in the current UK beef and sheep supply chain and the potential for genomic selection in traits not currently evaluated.

This Thesis has concentrated on evaluating the potential for GS within the existing industry breeding structures. In this section, this view is widened to include the entire beef and sheep meat supply chain in the UK. This aims to identify the drivers behind existing trait selection by breeders and highlight the key actors in the chain. The possibility of GS for novel traits, which were not previously examined in this Thesis, will be considered given the makeup of the supply chain.

7.3.1. The supply chain

The UK beef and sheep meat supply chain is illustrated in a generic form in Figure 7.1. This system is characterised by a lack of vertical integration (Mead, 2000; Cox *et al.* 2007). In other words, little information is sent back along the production chain from end

consumer, the meat eating public, to the disseminator of genetics, the pedigree beef and sheep breeder (Cox *et al.* 2007). It can be seen that the only signalling to extend throughout the entire chain is in the form of price premiums paid by supermarkets for carcasses from animals sired by certain UK native beef breeds (E.g. Morrisons, 2013). The meat is then sold as a 'branded breed product' to consumers. Chapter 2 estimated that less than 16% of prime beef cattle are sired by native breed bulls, and therefore even if all these animals were marketed through specialist schemes, these could only be considered as a niche sector of the market. The majority of the supply chain thus deals in 'commodity meat' and price signalling between the major actors in this case is limited to carcass weight and conformation. Therefore, the pedigree bull and ram breeders at the top are only incentivised (through prices achieved for breeding males) to select for these characteristics, and are not driven to select for traits desirable further down the supply chain such as meat quality. This is reflected in there only being evidence of selection, through genetic trends in pedigree breeding herds for growth rate and muscling traits.

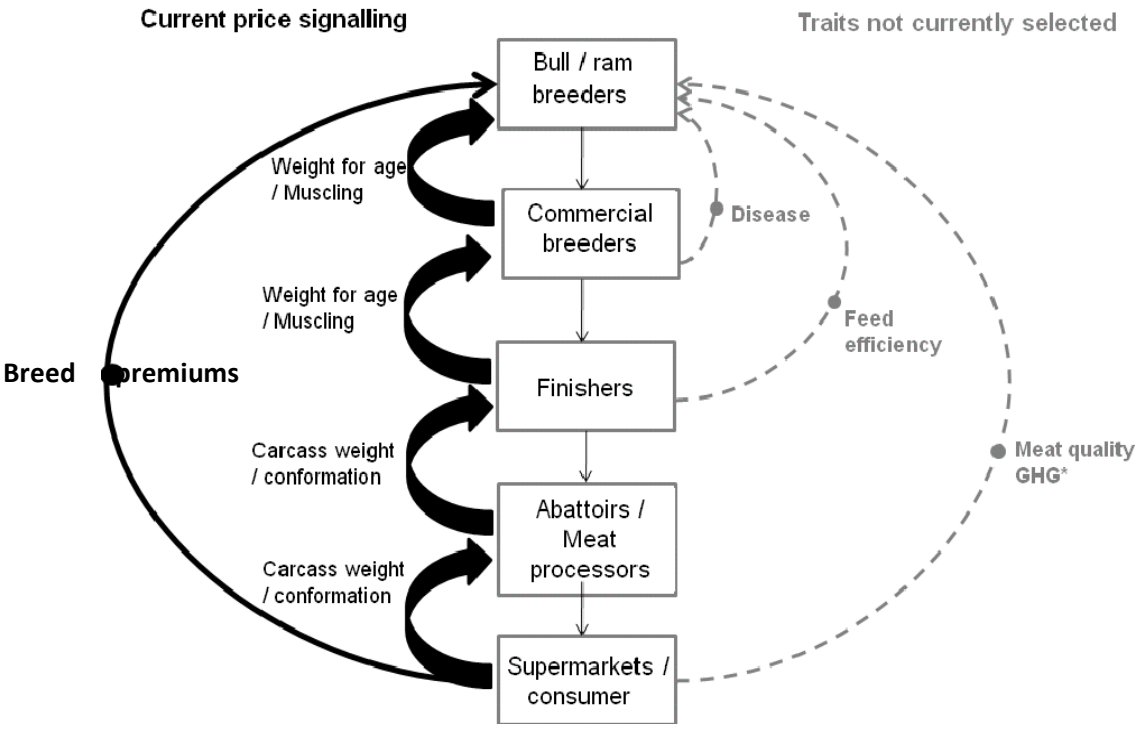

Figure 7.1 The UK beef and sheep meat supply chain. Current price signalling is indicated on the left in black, with the signalling route for four potential traits on the right in grey.

*GHG = greenhouse gas emissions

The most likely actors in the chain to drive further integration in the future are the powerful supermarkets (Mead, 2000; Cox *et al.* 2007; Leat and Revoredo-Giha, 2008). This power is excellently demonstrated by the 'Supply chain funnel' from Grievink (2003), which is reproduced in Figure 7.2. Whilst decision makers at the farmer and consumer level are vast in number, relatively few supermarkets control the buying and selling of, for example, meat.

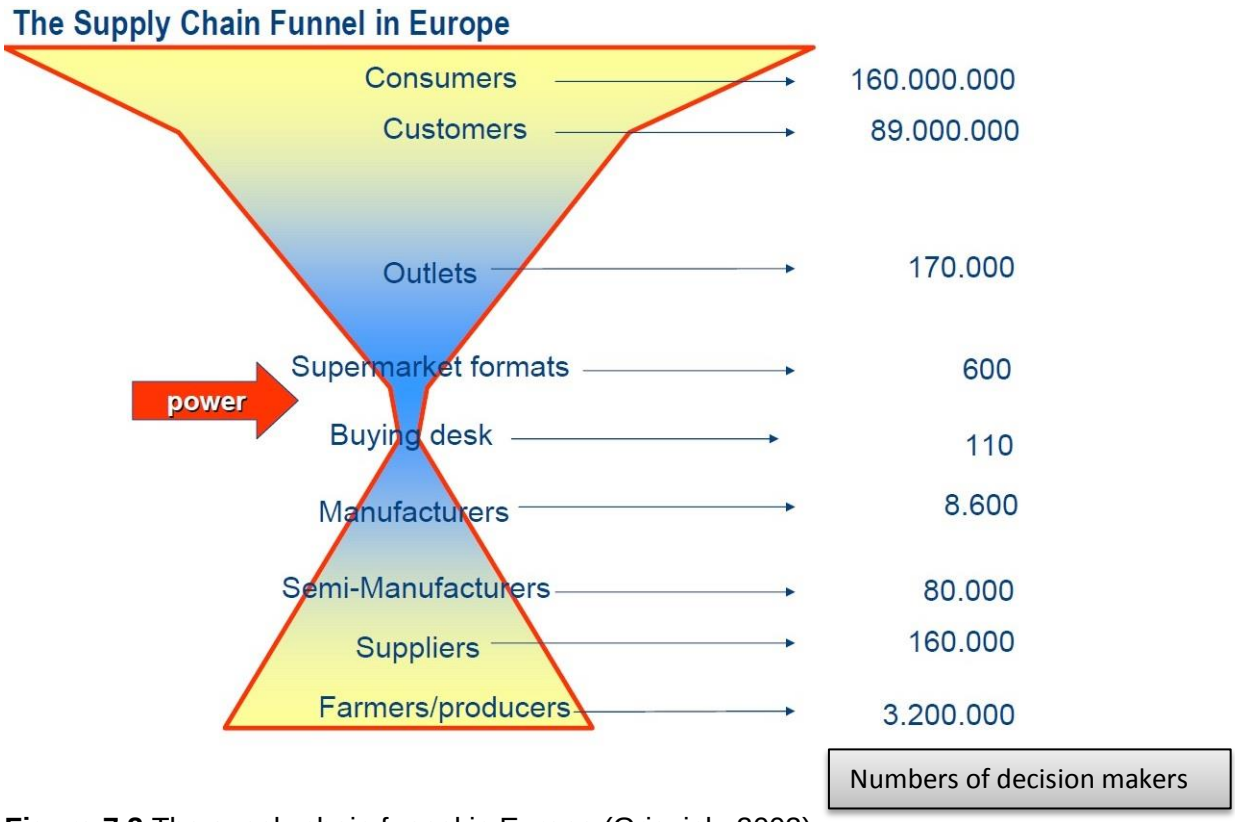

Figure 7.2 The supply chain funnel in Europe (Grievink, 2003)

Supermarkets have, through scale of activity, have become the dominant players in the supply chain. In contrast, farmers in Europe (and especially the UK) have mostly remained a disparate group of small businesses, largely competing with each other and thus not exerting a collective power over the supply chain. This has important implications for future trait selection in the UK, should supermarkets decide to exert more influence over beef and sheep breeding in the UK. Whilst Figure 7.1 adequately describes the supply chain in the majority of circumstances in the UK, i.e. as being non-integrated, a minority of activity is merged. For example, Fearne (1998) suggested that supply chain integration between 'producers, abattoirs and supermarkets' occurs in 20% of cases in the UK beef industry. Breeders have remained somewhat insulated by his lack of integration, and this is reflected in trait selection.

Box 7.1 Proportion of 'breeder-finishers'

In Chapter 2, the BCMS/SAC database provided extensive information on the lifetime events of beef cattle. In a further analysis of this database for this Discussion Chapter, 64% of prime age beef animals (aged 12 to 30 months at death in 2010), designated a having a beef-sired dam (i.e. a beef suckler cow) and a slaughter code, were denoted as having made more than two movements between animal holdings in their lifetimes, indicating that they were not owned by their breeder at time of death. It seems reasonable to assume that these cattle were 'finished' to slaughter by a second farmer. Movements between holdings of the same owner are not notifiable in BCMS (Green and Kao, 2007). Therefore, the remaining 38% of cattle would be bred to slaughter by 'breeder-finishers'. Leat and Revoredo-Giha (2008) provide supporting evidence for this analysis, in a survey of 611 Scottish beef and sheep farmers. Their study found that 60% of commercial beef breeders did not finish their cattle to slaughter. In contrast, only 38% of commercial sheep breeders did not take lambs through to slaughter. A lower estimate of beef 'breeder-finisher' numbers comes from EBLEX (2009) which suggests that 90% of suckler calves in England are sold after weaning, thus estimating breeder-finishers at only 10% of suckler farmers.

7.3.2 Commercial breeders and finishers. In figure 7.1, beef and sheep producers are separated into two further categories (commercial breeders and finishers). When considering drivers for trait selection it is important to identify how often the breeder and finisher roles are performed within one entity. The separation point between these two roles is traditionally at the weaning stage (EBLEX, 2009), with offspring separated from their mother for further rearing without milk and finishing for slaughter. Commercial farms where these activities are merged will breed animals and take them through to slaughter. Accurate data on the percentage of farmers engaged in both activities in the

UK is difficult to come by. Box 1 presents some evidence for the numbers of farms which do not engage in both activities in the UK. *These findings suggest that commercial breeders and finishers are mainly separate entities in the beef chain and mainly the same entity, the breeder-finisher, in the sheep chain.*

Given that commercial cattle do not have EBV in the UK, weaned calves cannot be selected by finishers on a basis other than colour, weight and muscularity (and limited parentage information through BCMS). Therefore, when purchasing replacement breeding bulls, the majority of commercial beef breeders are unlikely to be motivated to select for post-weaning traits which cannot be assessed by weight or visual appraisal, as this will not be financially incentivised within the existing supply chain. The exception to this would be in the case of maternal traits, which Chapter 2 demonstrated were at best actively selected for in only 7% of matings in suckler herds.

In contrast, buyers of breeding rams for commercial sheep production *will* typically be interested selection for post-weaning traits.

7.4. Future GS traits

Figure 7.1 includes four traits on the right hand side (feed efficiency, disease resistance, greenhouse gas production and meat quality which are not currently selected for in UK beef and sheep breeding. The actors likely to drive their selection for these traits are also identified (grey dashed arrows). These traits are among those commonly considered (e.g. as described in the introduction to the Discussion) as candidate traits for beef and sheep GS. These traits were not dealt with in the previous Chapters of this thesis and they will now be considered individually, with regard to their

likelihood of being adopted via GS, particularly in light of the analysis of factors driving selection in the supply chain, identified above.

7.4.1. Feed efficiency

Feed efficiency (FE) and its derived variants such as RFI (residual feed intake) are currently a major focus of research in animal science (Berry and Crowley, 2011). These are 'prima facia' an obvious area of GS interest given that they are novel traits, moderately heritable, expensive to measure on all selection candidates (Robinson *et al.* 2002, Herd *et al.* 2003) and with a potentially large economic impact (Van der Werf, 2009). FE research has concentrated on post–weaning stage animals, with no evidence in the literature of pre-weaning studies or of estimated genetic correlations with pre-weaning traits. The majority of commercial beef breeders, as described above, appear to have little incentive to select for post-weaning FE. In such circumstances, (commercial) buyers of breeding bulls are unlikely to place value on FE EBV. This was, for example, the finding of McDonald et al, (2010) when studying the sale of breeding bulls from a performance testing station in the USA which included feed efficiency among post-weaning traits measured. Only growth rate and calving ease EBV of bulls showed a positive relationship to sale price in that study. As observed by Van Eenennaam and Drake (2012), beef cattle are predominantly finished in feed lots in the USA, and thus the 'breeder-finisher' rarely exists in that country.

It is also suggested that RFI could be of interest in maternal selection (Crowley *et al.* 2011). However Chapters 2 and 5 of this Thesis demonstrated that very little intentional maternal selection occurs in the UK.

Implementing GS in RFI for UK breeder-finishers would need to overcome two major hurdles;

1) The use of a progeny test, such as modelled in Chapter 4, where a TP of 2000 pure-bred sires had around 40,000 progeny recorded in total, is implausible given the cost and impracticality. Alternatively pure-breds breeding animals could themselves be recorded for feed intake. This is also unlikely to be practical, given the small pedigree populations in the UK and the disease risk involved in grouping large numbers of these animals together from different herds. Therefore, the only solution would appear to be the development of a TP with genotypes and phenotypes from commercial cross-breds. As discussed in Chapter 4, the estimation of SNP effects in crossbred animals will likely be less accurate than it would in pure-breds, due to the increased presence of non-additive genetic effects. Ibanez-Escriche *et al.* (2009), for example, estimated that a cross-bred TP would require 4000 animals to achieve similar prediction accuracy as a pure-bred TP with 1000 animals, when validating in pure-breds and even with distantly related breeds. This assumed that the pure breed was represented in the admixture (which is common in the UK) and that SNP effects were the same multi-breed (which is only a hypothesis).

And

2) The cost of recording the phenotype, which was estimated by to be £1700 per animal in the UK, for a facility capable of testing 288 cattle per year (Roughsedge *et al.* , 2010). This would equate to £3.4 m for a TP of 2000 animals, although clearly a larger facility would be required to record such a number within a reasonable time period.

Box 2 compares the economic value of RFI selection in terminal beef breeding, predicted by Roughsedge *et al.* (2010), with the results for beef TI response in

Chapter 4. This analysis, suggests that implementation costs would outweigh the benefit from GS with a TI including RFI, even when assuming that all commercial breeders were motivated to select for this index with the same selection intensity currently observed for beef TI. Roughsedge *et al.* (2010) also investigated the correlated effects of GS for RFI on the carbon value of reduced GHG emissions by cattle, but found little commercial benefit in terminal beef breeding when taking into account implementation costs of RFI.

Box 7.2 RFI genetic gain

Roughsedge et al. (2010) predicted genetic gain from GS, when incorporating RFI in the Signet beef TI, using the same Ne and generation intervals as in Chapter 4. That study estimated 12% per year greater response in TI with GS than BLUP for TP = 2000, with GS in both sexes. This would equate to approximately £0.12 per animal per year in additional economic response, for the selection intensity currently observed in UK pedigree Limousin. In Chapter 4, an extra response of £0.28 per animal per year was predicted when using GS over conventional BLUP, which was projected to be worth £6.7 m, net of genotyping costs, over 20 years in Limousin sired terminal beef matings (with TP = 2000 and ρX = 0.7). Therefore, a response of £0.12 per animal would not justify the costs of phenotyping and genotyping 2000 animals for an RFI TP in the UK, even when applying RFI gain to all Limousin-sired terminal matings. Calculation; (£6.7 M x 0.12/0.28) - £3.4M = - £0.5M.

RFI is therefore unlikely to be a driver for GS implementation in beef in the UK.

In *contrast* to beef breeding, and as evidenced above, sheep are commonly bred and reared to slaughter age on the same farm. Paradoxically therefore, whilst most FE

research has involved cattle, it is arguable that more of a driver exists for potential adoption of selection for FE traits in sheep. Few studies have focused on selection for FE in sheep; Francois et al 2012 suggests (2002 WCGALP paper) that FE traits were moderately heritable in meat sheep while Sawalha *et al.* (2010) suggest GS for RFI could deliver worthwhile genetic gain. As with beef, the cost of phenotyping animals for RFI, in order to develop genomic TP would be the major hurdle to overcome if this trait were considered for GS in UK sheep (Sawalha *et al.* 2010). Adoption of GS in for FE traits in sheep does therefore appear possible; however, no facilities as yet exist in the UK for phenotype recording.

7.4.2. Greenhouse Gas emissions

Perhaps the livestock trait capturing the most public attention in recent years has been greenhouse gas emissions (GHG). Whilst animal breeding is postulated as a mitigation option (Alford *et al.* 2006; Hegarty *et al.* 2007), the nature of this trait dictates that it cannot be practically monitored, through widespread measurement of animal emissions on farms. A driver for implementation of GHG mitigation through breeding could come in the form of a penalty on meat production output, possibly via subsidy adjustment. Hence, farmers would be driven to produce each kilo of animal meat more efficiently and thus select for traits which would, by genetic correlation, also reduce GHG, such as FE and growth rate. Whilst the difficulties in implementing the former trait in the UK are outlined above, growth rate is a potential proxy-trait which farmers could select for and reduce emissions simply by reducing time to slaughter of prime animals (Jones *et al.* 2008). One issue with the use of growth rate as a proxy trait is that it can also increase mature cow size (Koots *et al.* 1994), and thus increase GHG emissions in adult animals (Roughsedge *et al.* 2010). This would not be an issue for those UK beef breeds,

identified in Chapter 2, supplying breeding bulls which only have a small percentage of commercial females retained for breeding, notably Charolais, Blonde and arguably Limousin. Each of these breeds has a smaller (by percentage) genetic contribution to the suckler herd than the prime slaughter population (see Tables 2 and 6, Chapter 3). Similarly, terminal sire sheep breeds, such as Texel, have a much lower genetic contribution to breeding ewe populations than to the prime lamb population (Pollott and Stone, 2006).

Therefore, if breeding is seen as a GHG mitigation tool in the UK, this is likely to be implemented through selection for improved growth rate, which was dealt with in Chapters 4 and 6 of this Thesis.

7.4.3. Meat quality

Whilst the consistency of meat quality appears to be a substantial concern for supermarkets and consumers (Mead, 2000; Cox *et al.* 2007; Leat and Revoredo-Giha, 2008) traits such as tenderness and flavour are not routinely recorded in UK abattoirs, and thus not selected for by breeders. Van Eenennaam *et al.* (2011) and Pimentel and Konig (2012) both explored GS for meat quality in beef cattle, and both concluded that GS could substantially increase genetic gain in these traits. The implementation route would likely be a similar to that proposed for the carcass traits in Chapter 4. However, as noted by Van Eenennaam *et al.* (2011), greater vertical integration of the supply chain than currently exists would be required to drive implementation of GS for meat quality.

7.4.4. Disease resistance

Disease has been the single most important issue in UK livestock production over the last 20 years. A number of serious outbreaks, most notably BSE, Scrapie, Foot and

mouth, Bovine Tb and Johnes have afflicted, and continue to afflict, cattle and sheep populations. GS has been proposed as a viable and attractive method of selecting for disease resistance in other species, notably farmed fish (Nirea *et al.* 2012) and poultry (Fulton, 2012). Selection in these species is largely driven by breeding companies with control over breeding populations. TP in these species can be developed using relatively low value breeding animals (or close relatives e.g. siblings or half siblings), which can be disease challenged in controlled environments. Deliberately inoculating a TP (involving thousands of animals) with disease traits appears less feasible in beef and sheep, especially given the high value of breeding animals and the risks involved with infected animals in a grazing environment. Developing TP in commercial herds and flocks could be a solution for less infectious diseases, measured by values close to 1 of the basic reproductive ratio R_0 (Bishop and Gettingby, 2000). Epidemics of diseases with high R_0 such as foot and mouth are unlikely to be prevented by selection for disease resistance in contrast to those with lower R_0**.** However**,** estimating response to selection for disease resistance can be problematic. For example with gastrointestinal worms, the presence of a disease resistant animals in a grazing group reduces the potential for other animals to be challenged (Bishop, 2012). It seems more likely that disease recording and organised DNA sampling in existing populations would need to be developed to enable GS for disease resistance (Bishop *et al.* 2012).

Bovine Tb is an obvious candidate for GS, given that it is (moderately) heritable (Berry *et al*. 2011), has an R_0 close to 1 (Cox *et al*. 2005), a large economic cost to the UK (Davies *et al*. 2005) and that it currently infects substantial numbers of cattle in the UK on an on-going annual basis, thus providing ample opportunity for phenotypic recording. The politically sensitive nature of this disease in the UK is an added complication when

considering publication of for example GBV for valuable sires. However, one of the key reasons for this sensitivity, the huge economic cost, may dictate that GS becomes a necessary tool in combating Bovine Tb.

An important precedent for DNA-based selection of disease resistance exists in the UK with Scrapie in sheep. Selection to eradicate alleles associated with susceptibility to this disease saw 'widespread uptake through the pure-breeding sector' (Dawson *et al.,* 2008). This example aptly demonstrates that if a strong enough driver exists (in this case the threat of association between Scrapie with BSE), and selection is effective in conferring disease resistance, then DNA-based selection disease resistance would be adopted by livestock breeders. Such is the impact of disease in UK livestock populations that GS for disease resistance in beef and sheep must be considered as a potentially powerful future driver for GS implementation, albeit one which may only involve the breeder-finisher tiers in Figure 7.1.

7.4.5. Conclusion to trait selection

If the supply chain remains fragmented in the future, it is difficult to envisage a change in trait selection by beef and sheep breeders, particularly towards characteristics not directly wanted by breeders purchasing males for commercial breeding (Van Eenennaam *et al.* 2011). It is commonly postulated that GS (e.g. Dekkers, 2009) has the potential to drive change in the supply chain and increase the level of vertical integration, because this technology can facilitate selection of novel or difficult to measure traits. The carcass and CT traits investigated in Chapters 4 and 6 of this thesis are examples of this concept. The analysis in this section supports an uptake of CT trait selection as proposed in Chapter 6, at least on the basis of sheep breeder-finishers being driven to select for carcass traits. It is less clear that all beef breeders would

necessarily be driven to select for the carcass goal traits in Chapter 3. The selection intensity adopted in this Chapter takes this into account and furthermore the key carcass trait, carcass weight is positively correlated (0.50) with one of the key pre-weaning traits, 200 day weight.

However, there seems little likelihood of adoption of other, often postulated candidate traits for GS (e.g. FE, GHG and Meat quality), without greater vertical integration of the supply chain, which is also the view of Van Eenennaam and Drake, (2012). It seems more likely, in the case of the UK, that greater supply chain integration would drive GS selection for most novel traits, rather than the other way round.

7.5. Future possibilities of genomic selection

7.5.1. Opportunities for international cooperation

This Thesis has concentrated on the feasibility of developing genomic TP within the UK. International cooperation in TP may be an avenue which could facilitate GS in the UK, for those traits or breeds with insufficient phenotypes for effective genomic prediction. Chapter 3 demonstrated that the Limousin breed in the UK has strong genetic links with the French population in particular. This is also likely to be the case for the UK Angus and Hereford herdbooks (with North American populations) and the British Blue (with the Belgian Blue). However, in other beef and sheep breeds, it appears that at best only a handful of international sires' genotypes could be used in augmenting UK TP. For those populations with genetic links, international cooperation could also extend to the sharing of phenotypes. This would be especially useful in traits which are expensive to measure such as FE and GHG. The value of international phenotypes will depend on

the extent of G x E between countries and the commonality of protocols for trait measurement (i.e. is the same phenotype being measured in the same way in both countries). The lower the genetic correlation between countries, the less accurate the phenotype.

7.5.2. Multi-breed prediction

The ability to develop an accurate multi-breed genomic predictor in the UK, would likely have major implications for beef and sheep breeding. The ability to compare genetic merit of all animals in a population, whether pure-bred or cross-bred could lead to a substantial re-assessment of breed use in the UK beef and sheep sectors. Such comparison is not available with current genetic evaluations in the UK, with breeds split between two independent providers (ABRI and BASCO). Objective comparison between breeds is therefore not possible, and this must in part explain the breed diversity observed in the UK. It is highly unlikely that the diversity of breeds with substantial genetic contributions to the prime beef population, described in Chapter 2 of this thesis, constitutes efficient beef breeding. In contrast, sheep breed use in the UK is more linked to topography and it is unlikely that one or two breeds could fulfil all roles. The general consensus in the literature suggests that the 50K marker panels are not dense enough to predict multi-breed GBV with useful accuracy in beef and sheep (Garrick, 2011; Pollak *et al.* 2012). It is postulated that the 700-800K marker panels (now commonly referred to as ‘HD’ chips) recently developed, will be dense enough to enable effective multi-breed evaluation. However practical evidence of this does not yet exist in the literature (as of early 2013). It may be that multi-breed selection will only be possible with full sequencing, where causal mutations are genotyped rather than genetic markers in LD.

7.5.3. The end of pedigree?

The ultimate concept of GS in livestock breeding, if sufficient selection accuracy can be obtained from genotyping alone (i.e. GBV used rather than GEBV), does not require pedigree information. For example, carcass traits in beef cattle could be selected solely through the genotyping of breeding bulls and routine collection of abattoir phenotypes. Initially, this could catalyse selection within pure-bred (but not pedigree registered) herds as suggested by Saatchi *et al.* (2012). It is perhaps ironic therefore, that pedigree herdbooks are playing a central role in beef GS adoption (Garrick, 2011). Breed societies contemplating GS in the UK may wish to consider the future possibilities of the technology. On the one hand, the first breed to develop GS (Limousin in the UK) may gain a competitive advantage and increase market share. On the other hand, successful GS by a breed society may serve to promote the possibilities of the technology to a wider beef audience, and (with technological advance) accelerate the demise of the pedigree concept. Whilst pedigree breeding in the UK has not been associated with particularly efficient selection, it has helped to maintain a great diversity of beef and sheep breeds. GS is postulated to maintain within-breed diversity more effectively than BLUP (E.g. Daetwyler *et al.* 2007; Dekkers, 2007a). However the use of genotyping technology ultimately has the potential to greatly decrease genetic diversity in species as a whole, by more accurately comparing genetic merit between breeds currently used for the same purpose, and thus reducing the number of breeds involved in (commodity) beef and sheep meat production.

7.6. Conclusion and recommendations for industry

Beef. This thesis explored both commercial and pedigree UK beef breeding populations in considerable detail, which enabled an informed and objective study of the potential merit of GS. This technology can facilitate the inclusion of commercial carcass phenotypes in pedigree evaluations, resulting in more efficient and accurate selection and thus greater genetic response. Gain achieved through increased selection accuracy alone would economically justify implementation. Adoption of GS via this route is therefore recommended and could provide a platform for evaluation of further traits in the future, particularly if further supply chain integration occurs and if effective multi-breed genomic prediction is developed.

Three key steps are required to implement this concept.

1) Routine collection of DNA on an annual basis from (ideally at least 1000) young pedigree beef bulls to sale to commercial herds. Ideally this would take place at official breed society sales.
2) The establishment of DNA repositories by breed societies to safely store this material over a long term period.
3) Joining up of information between abattoir, BCMS and pedigree Databases. Increased recording of sire identification in BCMS is the key parameter needed optimise this information chain.

Sheep. Building upon existing knowledge of commercial sheep populations, this thesis identified an opportunity for GS to harness the potential of a powerful phenotyping technology, computer tomography. The synergy between these technologies was predicted to result in gain with commercial value in excess of implementation costs. However, considering the lack of evidence for use of existing EBV technology in UK commercial sheep breeding, this scheme is considered as being of greater *risk* than the beef carcass concept. Consequently, it is recommended that Terminal sheep breeds considering the implementation of GS delay until a significant decrease in genotyping costs occurs, thus reducing the economic risk involved with this scheme.

References

AHDB, Agriculture and horticulture development board. 2011. A pocketful of meat facts. ADHB, Stoneleigh, UK.

Alford, A. R., Hegarty, R. S., Parnell, P. F., Cacho, O. J., Herd, R. M., and Griffith, G. R. (2006). The impact of breeding to reduce residual feed intake on enteric methane emissions from the Australian beef industry. Australian Journal of Experimental Agriculture 46 (6-7), 813-820

Allen D 1990. Planned beef production. BSP Professional Books, Oxford, UK.

Amer PR, Crump R, and Simm G. 1998. A terminal sire selection index for UK beef cattle. Journal of Animal Science 67,445-454.

Amer, P. R., Lowman, B.G. and Simm, G. (1998). Economic values for reproduction traits in beef suckler herds based on a calving distribution model. Livestock Production Science 46, 85-96.

Amer, P.R., Niewhof, G.J., Pollott, G.E, Roughsedge, T., Connington, J. and Simm, G. 2007. Industry benefits from recent genetic progress in sheep and beef populations. Animal. 1:10, 1414-1426.

American Angus Association, 2012. Genomic evaluations. Retrieved July 10, 2012, from http http://www.angus.org/Nce/WeeklyEvalGenomicData.aspx.html

Andrew Cox, Daniel Chicksand, Martin Palmer, (2007) "Stairways to heaven or treadmills to oblivion?: Creating sustainable strategies in red meat supply chains", British Food Journal, Vol. 109 Iss: 9, pp.689 – 720.

Andrew Fearne, (1998) "The evolution of partnerships in the meat supply chain: insights from the British beef industry", Supply Chain Management: An International Journal, Vol. 3 Iss: 4, pp.214 – 231.

Arthur, P.F. 1995. Double muscling in cattle: a review. Australian Journal of Agricultural Research, 46(8); 1493 – 1515.

BASCO 2010. UK animal registration numbers. Retrieved January 25, 2010, from http://www.egenes.co.uk/bascosearchbeef/

BASCO. 2011. Limousin pedigree genetic evaluation records. Retrieved November 25, 2011, http://www.basco.org/.

BASCO 2012. Limousin pedigree genetic evaluation records. BASCO database, EGENES, Edinburgh.

BBCS (British Blue Cattle Society). Yearbook 2009. BBCS, Penrith, UK.

BCCS (British Charolais Cattle Society). Yearbook 2009. BCCS. Stoneleigh, UK.

BCMS (British Cattle Movement Service). 2009. Cattle keeper's handbook ,version 3. BCMS, Workington, UK.

Berry, D.P, Bermingham, M.L., Good, M. and Moore, S.J. 2011 Genetics of animal health and disease in cattle Irish Veterinary Journal, 64:5. http://www.irishvetjournal.org/content/64/1/5.

Bichard, M. 1971. Dissemination of genetic improvement through a livestock industry. Animal production, 13 (3), 401-411.

Big Beef. 2012 http://www.bigbeef.co.uk/. Retrieved January 1, 2012, from http://www.bigbeef.co.uk/.

Bijma P, and van Arendonk J.AM 1998. Maximising genetic gain for sire line of a crossbreeding scheme utilizing both purebred and crossbred information. Animal Science, 66, 529-542.

Bijma. P. 2012. Accuracies of estimated breeding values from ordinary genetic evaluations do not reflect the correlation between true and estimated breeding values in selected populations. Journal of Animal Breeding and Genetics. 129(5):345-58.

Bishop, S.C. and Gettingby, G. 2000. Modelling Farm Animal Diseases, in Breeding for Disease Resistance in Farm Animals 7th. Editors; Axford, R.F.E, Bishop, S.C., Nicholas, F.W. and Owen, J.B.

Bishop, S. and Woolliams, J.A. 2004. Genetic approaches and technologies for improving the sustainability of livestock production. Journal of the Science of Food and Agriculture 84, 911-919.

Bishop SC, Doeschl-Wilson AB and Woolliams JA (2012) Uses and implications of field disease data for livestock genomic and genetics studies. Frontiers in livestock genetics, 3:114.

BLCS (British Limousin Cattle Society). Studbook and Factfinder 2006. BLCS. Stoneleigh, UK.

BLCS (British Limousin Cattle Society). Studbook and Factfinder 2009. BLCS. Stoneleigh, UK.

BLCS 2011. BLCS (British Limousin Cattle Society). Limousin News, British Limousin Cattle Society, Stoneleigh, UK.

BLCS 2012. BLCS (British Limousin Cattle Society). Studbook and Factfinder 2011. BLCS. Stoneleigh, UK.

Bouquet, A., Venot, E., Laloë, D., Forabosco, F., Fogh, A., Pabiou, T., Moore, K., Eriksson, J.Å., Renand, G. and Phocas, F. 2011. Genetic structure of the European Charolais and Limousin cattle metapopulations using pedigree analyses. Journal of Animal Science. 89(6);1719-30.

Bourdon, R.M. 2000. Understanding animal breeding. 2nd. Prentice Hall Inc. New Jersey, USA.

Breedplan 2010. UK animal registration numbers. Retrieved January 25, 2010, from http://breedplan.une.edu.au/

Breedplan. 2012. Genetic evaluation records. Retrieved November 1, 2012, from http://breedplan.une.edu.au/.

Brito FV, Braccini Neto JB, Sargolzaei M, Cobuci JA, and Schenkel FS, 2011. Accuracy of genomic selection in simulated populations mimicking the extent of linkage disequilibrium in beef cattle. BMC Genetics, 12:80.

BTSS (British Texel sheep society) 2012a. Texel sheep society journal. BTSS, Stoneleigh, UK.

BTSS (British Texel sheep society) 2012b. Performance recording your Texel flock. BTSS, Stoneleigh, UK.

Bulmer, M.G. 1971. The effect of selection on genetic variability. American Naturalist, 105 (943); 201-211.

Bunger, L. , Macfarlane, J M. , Lambe, N R. , Conington, J. , McLean, K A. , Moore, K. , Glasbey, C A . , and Simm, G. 2011. Use of X-ray computed tomography (CT) in UK sheep production and breeding. CT Scanning – Techniques and Applications (Karuppasamy, S . ,) pp. 329-348, INTECH Open access Publisher.

Calus, M.P.L. 2009 Genomic breeding value prediction: methods and procedures. Animal, 4: 2, 157-164.

CEEU (Central expenditure evaluation unit), 2011. Comprehensive Review of Expenditure 2011,CEEU Paper No.6, Overview of 'Legacy' Expenditure Programmes and Policy Reforms,including opportunities for rationalising State Agencies. Retrieved January 29, 2012, from / http://per.gov.ie/wp-content/.

Charlier C., Coppieters W., Farnir F., Grobet L., Leroy P. L., Michaux C., Mni M., Schwers A., Vanmanshoven P., Hanset R., Georges M.1995. The mh gene causing double-muscling in cattle maps to bovine Chromosome 2. Mammalian Genome 6:788–792.

Cockett, N.E., Jackson, S.P., Shay, T.L., Nielsen, D., Moore, S.S., Steele, M.R., Barendse, W, Green, R.D., and Georges, M. 1994. Chromosomal localization of the callipyge gene in sheep (Ovis aries) using bovine DNA markers. PNAS 1994 91 (8) 3019-3023.

Cox, D. R., Donnelly, C.A., Bourne, F.J., Gettinby, G., McInerney, J.P., Morrison, I.W. and Woodroffe, R. 2005. Simple model for tuberculosis in cattle and badgers. PNAS, 102 (49) 17588-17593.

Craven JA and Kilkenny JB 1976. The structure of the British cattle industry. In Principles of Cattle Production (eds Swan H and Broster WH), 1-37. Butterworths, London, UK.

Cromie AR, Amer P, Veerkamp RF, Berry DP**,** and Wickham B (2010). The theory of genetics applied to livestock production : some experiences from Ireland. In: 9th World Congress on Genetics Applied to Livestock Production, Leipzig, Germany 0949, 1-4.

Crowley JJ, Evans RD, Mc Hugh N, Kenny DA, McGee M, Crews DH Jr and Berry DP.J. 2011 Genetic relationships between feed efficiency in growing males and beef cow performance. Animal Science, 89(11):3372-81.

François, D., Bibé, B., Bouix, J., Brunel, J.C., Weisbecker, J.L., Ricard, E. 2002. Genetic parameters of feeding traits in meat sheep. Proceeding of the 7th World Congress of Genetics Applied to Livestock Production. Montpellier, France. Comm. No. 10-10.

Berry, D. P. and Crowley, J. J.. 2011.Residual intake and body weight gain: A new measure of efficiency in growing cattle. J ANIM SCI 2012, 90:109-115.

Daetwyler H .2009. Genome-Wide evaluation of populations. PhD. Wageningen University, the Netherlands.

Daetwyler HD, Villanueva B, and Woolliams J A, 2008. Accuracy of Predicting the Genetic Risk of Disease Using a Genome-Wide Approach. Plos One 3(10), e3395.

Daetwyler, H.D., Villanueva, B., Bijma, P. and Woolliams, J.A. 2007. Inbreeding in genome-wide selection. Journal of Animal Breeding and Genetics, 124; 369-376.

Daetwyler HD, Swan AA, van der Werf JH, Hayes BJ. 2012. Accuracy of pedigree and genomic predictions of carcass and novel meat quality traits in multi-breed sheep data assessed by cross-validation. Genetics Selection Evolution, 12;44:33. doi: 10.1186/1297-9686-44-33.

Davies, G. Genini, S. Bishop, S.C. and Giuffra. 2009. An assessment of opportunities to dissect host variation in resistance to infectious diseases in livestock. Animal, 3(3), 415-436.

Dawson M, Moore RC, Bishop SC. 2008. Progress and limits of PrP gene selection policy. Veterinary Research. 39 (4).

De Roos, A.P.W., Hayes, B.J. and Goddard, A.P.W., Hayes, B.J., Spelman, R.J. and Goddard, M.E. 2009. Reliability of genomic predictions across multiple populations. Genetics. 183, 1545-1553.

Defra 2004. June Survey of Agriculture and Horticulture. Defra, London, UK.

Defra 2006. Agriculture in the United Kingdom, Defra, London, UK.

Defra (a) 2008. Agriculture in the United Kingdom. Defra, London, UK.

Defra (b) 2008. The Cattle Book 2008. Defra, London, UK.

Defra 2010. UK Slaughter Statistics. Retrieved February 1, 2010, from http://statistics.Defra.gov.uk/esg/slaughterns.htm

Defra. 2012a. UK sheep numbers historical June survey. Retrieved June 6, 2012, from http://www.defra.gov.uk.

Defra. 2012b. EID in sheep. Retrieved June 6, 2012 from http://www.defra.gov.uk/food-farm/animals/movements/sheep/.

Dekkers JCM 2007a. Prediction of response of marker-assisted and genomic selection using selection index theory. Journal of Animal Breeding Genetics 124, 331-341.

Dekkers JCM 2007b. Marker-assisted selection for commercial crossbred performance. Journal of Animal Science 85, 2104-2114.

Dekkers, J.C.M. 1992. Asymptotic response to selection on best linear unbiased prediction of breeding values. Animal Production, 54; 351-360.

Deukwhan L, and Vasco A, 2011. Predicting the accuracy of breeding values using high density genome scans. Asian-Australasian Journal of Animal Science 24(2), 162-172.

Drennan, M.J. ,McGee, M. and Keane, M.G. 2005. Post-weaning performance and carcass characteristics of steer progeny from different suckler cow breed types. Irish Journal of Agricultural and Food Research. 44, 195-204.

Drennan, M.J. and Berry, D.P. 2006. Factors affecting body condition score, live weight and reproductive performance in spring-calving suckler cows. Irish Journal of Agricultural and Food Research. 45, 25-38.

EBLEX. 2009. In the balance? The future of the English beef industry. EBLEX, Warwickshire, UK.

EBLEX, 2011. UK meat and livestock yearbook. EBLEX, Kenilworth, UK.

EBLEX 2012. Beef cattle prices 2010-2012. Retrieved September 1, 2012 from http://www.eblex.org.uk/markets/.html

EBLEX 2012, Texel genetic trends. EBLEX, Kenilworth, UK.
EBLEX. 2012. UK livestock market price. Retrieved September 1, 2012 from http://www.eblex.org.uk/markets/.

Edwards J, Jobst D, Hodges J, Leyburn M, O'Connor LK, Macdonald A, Smith GF and Wood P 1966. The Charolais report. Milk Marketing Board, Thames Ditton.

Eriksson, S., Nasholm, A., Johansson, K., and Philipsson, J. 2004. Genetic parameters for calving difficulty, stillbirth, and birth weight for Hereford and Charolais at first and later parities. Journal of Animal Science, 82(2); 375-383.

Falconer, D.S. and Mackay, F.C. 1996. Introduction to Quantitative Genetics (4th edition). Pearson Education LTD. Harlow, UK.

FAO (Food and Agriculture Organization), 1998. Secondary guidelines for development of national farm genetic resources management plans: management of small populations at risk. FAO, Rome, Italy.

Fouilloux, M., Renand, G., Gaillard, J. and Menissier, F. Genetic parameters of beef traits of Limousin and Charolais progeny-tested AI sires. Genetics Selection Evolution, 31: 465-489.

Fulton J. E. 2012. Genomic selection for poultry breeding. Animal Frontiers 2012 2:30-36

Garrick DJ, 2011. The nature, scope and impact of genomic prediction in beef cattle in the United States. Genetics Selection Evolution 43:17.

Gembal, 2012. Multi-breed Genomics of Beef and Dairy Cattle in France. Retrieved November 10, 2102 from http://www.agence-nationale-recherche.fr/programmes-de-recherche/environnement-et-ressources-biologiques/adaptation-des-genes-aux-populations-genetique-et-biologie-de-ladaptation-aux-stress-et-aux-perturbations/fiche-projet-genom-btv/?tx_lwmsuivibilan_pi2%5BCODE%5D=ANR-10-GENM-0014.

Genomes Canada. 2012. Genomic selection in beef cattle. Retrieved November 1 2012 from http://www.genomecanada.ca/en/portfolio/research/bovine.aspx.

Gibbs D, Holloway L, Gilna B and Morris C 2009. Genetic techniques for livestock breeding: restructuring institutional relationships in agriculture. Geoforum 40, 1041-1049.
Goddard, M.E. and Hayes, B.J. 2009. Mapping genes for complex traits in domestic animals and their use in breeding programmes. Nature Reviews Genetics 10, 381-39, doi:10.1038/nrg2575.

Green, D. M. and Kao R. R. 2007. Data quality of the Cattle Tracing System in Great Britain. Veterinary Record, 161:13, 439-443.

Gregory KE, Cundiff LV and Koch RM 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. Journal of Animal Science, 73:1920-1926.

Grievink, J. 2003. The supply chain funnel, Cap Gemini report for OECD.

Grobet, L., Poncelet, D., Royo, L. J., Brouwers, B., Pirottin, D., Michaux, C., Ménissier, F., Zanotti, M., Dunner, S., Georges, M. 1998. Molecular definition of an allelic series of mutations disrupting the myostatin function and causing double-muscling in cattle. Mammalian Genome 9:210–213.

Habier, D. Fernando, R. L. and Dekkers, J. C. M. 2009. Genomic Selection Using Low-Density Marker Panels. Genetics, 182:343-353.

Haley, C.S. and Visscher, P.M. Strategies to Utilize Marker-Quantitative Trait Loci Associations. Journal of Dairy Science, 81, 85-97.

Hall J G and Clutton-Brock J. 1989. Two hundred years of British livestock. Craft Print, Singapore.

Hayes, B.J., Bowman, P.J., Daetwyler, H.D., Kijas, J.W., van der Werf, J.H. 2012. Accuracy of genotype imputation in sheep breeds. Animal Genetics. 43(1):72-80. doi: 10.1111.

Hegarty, R. S., Goopy, J. P., Herd, R. M., and McCorkell, B. (2007). Cattle selected for lower residual feed intake have reduced daily methane production. Journal of Animal Science 85 (6), 1479-1486.

Henderson, C.R. (1975). Best linear unbiased estimation and prediction under a selection model. Biometrics 31 (2): 423–447.

Henryon M, Berg P, Ostersen T, Nielsen B, Sørensen AC. 2012. Most of the benefits from genomic selection can be realized by genotyping a small proportion of available selection candidates. Journal of Animal Science 90, 4681- 4689.

Hickey JM, Keane MG, Kenny DA, Cromie AR and Veerkamp, RF 2007. Genetic parameters for EUROP carcass traits within different groups of cattle in Ireland. Journal of Animal Science 85, 314-321.

Hill, W.G. 2010. Understanding and using quantitative genetic variation. Philosophical transactions of The Royal Society of Biological Sciences, 365; 73-85.

HM Treasury 2012.Green Book. Retrieved July 10, 2012, from http://www.hmtreasury.gov/uk /d/green_book_complete.pdf.html.

Hoards Dairyman 2011. Genomics is being adopted at a swift pace. March 10, 164. W.D. Hoard and Sons, Wisconsin, USA.

Holstein International. 2012. Genomic bulls, how do users select them? November, 10-11. Holstein International BV, Stiens, the Netherlands.

Huang, Y., Hickey, J.M., Cleveland, M.A. and Maltecca, C. 2012. Assessment of alternative genotyping strategies to maximize imputation accuracy at minimal cost. Genetics Selection Evolution 31;44:25. doi: 10.1186/1297-9686-44-25.

Ibanez-Erische, N., Fernando, R.L., Toosi, A. and Dekkers, J.C.M. 2009. Genomic selection of purebreds for crossbred performance. Genetics Selection Evolution. 41, 12.

ICBF (Irish Cattle Breeders Federation). 2010.Beef breeding in Ireland. ICBF, Cork, Ireland.

Jobst D, 1986. Limousin cattle in the United Kingdom. Keystock Associates LTD, Surrey. UK.

Jones, HE, Warkup, CC, Williams, A, Audsley, E 2008. The effect of genetic improvement on emission from livestock systems. In Proceedings of the European Association of Animal Production, 24–27 August 2008, Vilnius, Lithuania, Session 5.6, p. 28.

Jorjani H, Klei L and Emanuelson U 2003. A simple method for weighted bending of genetic (co)variance matrices. Journal of Dairy Science 86, 677-679.

Keeble M 2004. Limousin, the breed, the people, the story. Keeble, Ripon, UK.

Kijas JW, Lenstra JA, Hayes B, Boitard S and Porto Neto LR. 2012. Genome-Wide Analysis of the World's Sheep Breeds Reveals High Levels of Historic Mixture and Strong Recent Selection. PLoS Biol 10(2): e1001258. doi:10.1371/journal.pbio.1001258

Kirkland, R.M. and Keady,T.W.J. Agrisearch, 2004. The influence of suckler cow genetics and terminal sire on performance of the suckler herd. Agrisearch (booklet No8), Hillsborough, Northern Ireland.

Konig S and Swalve HH. 2009. Application of selection index calculations to determine selection strategies in genomic breeding programs. Journal of Dairy Science 92, 5292-5303.

Koots, K. R., Gibson, J. P., and Wilton, J. W. (1994b). Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Animal Breeding Abstracts 62, 825-853.

Koots, K.R. and Crow, G.H. 1989. Breed structure of pedigreed Hereford cattle in Canada. Canadian Journal of Animal Science, 69; 627-634.

Limousin and Simmental Tests Steering Committee, 1976. Limousin and Simmental Tests Steering Committee, Report of the evaluation of the first importation into Great Britain in 1970/71 of Limousin bulls from France and Simmental bulls from Germany and Switzerland. HMSO, London (1976).

Lowman B 1998. The past, present and future for UK suckler herds. Cattle Practice 6, 155-161.

Lowman BG 1997. Description of the UK beef industry, structure and production systems. Cattle Practice 5, 145-147.

Lowman, B.G., 1997. Description of the UK beef industry, structure and production systems. Cattle Practice, 5(2).

Lush, J. L. 1937. Animal breeding plans. Iowa State College Press, Ames, Iowa.

Maddox, J.F. and N.E. Cockett. (2007). An update on sheep and goat linkage maps and other genomics resources. Small Ruminant Resources. 70:4-20.

Marquez, G.C and Garrick D.J. 2007. Selection intensities, generation intervals and population structure of Red Angus cattle. Proceedings of the American Society of Animal Science Western Section 58, 55-58.

Marquez, G.C., Speidel, E.S., Enns, R.M and Garrick D.J. 2009. Genetic diversity and population structure of American Red Angus cattle. Journal of Animal Science, 88: 59-68.
maternal breeding goal and tools to select for this goal in UK beef production. Animal Science 81**,** 221-232.

McClure MC, McKay S D, Rolf MM, Kim J, Decker J E, Taxis T M, Chapple R H, Ramey R, Northcutt S L, Bauck S, Woodward B, Dekkers J C M, Fernando R L, Schnabel R D, Garrick DJ, and Taylor, J F. 2011. Accuracies of genomic breeding values in American Angus beef cattle using K-means clustering for cross-validation. Genetic Selection Evolution 43:40.

McGee, M., Drennan, M.J. and Caffrey, P.J. 2005. Effect of suckler cow genotype on milk yield and pre-weaning calf performance. Irish Journal of Agricultural and Food Research. 44, 185-194.

McParland, s, Kearney,M.,Rath, M and Berry, D. 2007. Inbreeding trends and pedigree analysis of Irish dairy and beefcattle populations . Journal of Animal Science, 85; 322-331.
Mead, S. 2000. Strategic analysis of the British beef industry. Cattle practice, 8(2); 71-73.

Meuwissen, T.H.E. 2009. Accuracy of breeding values of ‘unrelated’ individuals predicted by dense SNP genotyping. Genetics Selection Evolution 41:35.

Meuwissen, T.H.E., Hayes,B.J. and Goddard,M.E., 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics, 157, 1819-1829.

Mistzal, I. 2006. Challenges of application of markers assisted selection – a review. Animal Science Papers and Reports, 24:1, 5-10.

Misztal, I., Legarra, A. and Aguilar, I. 2009. Computing procedures for genetic evaluation including phenotypic, full pedigree, and genomic information. Journal of Dairy Science, 92, 4648–4655.

MLC (Meat and Livestock Commission). 1990. UK Meat and Livestock Yearbook. MLC, Milton Keynes, UK.

MLC (Meat and Livestock Commission) 1993. Beef Yearbook. MLC, Milton Keynes.UK.

MLC (Meat and Livestock Commission) 2008. UK Meat and Livestock Yearbook. MLC. Milton Keynes, UK.

MLC (Meat and Livestock Commission) 2008. UK Meat and Livestock Yearbook. MLC. Milton Keynes, UK.

Moore, K., Mrode, R., Coffey, M., Lowman, B., Hill, G. and Roughsedge, T. 2010. Demonstrating the benefits of using maternal EBVs in selecting beef sire. Scottish Agricultural College, Edinburgh, UK. (report commissioned by Quality Meat Scotland).

Morrisons 2013. Morrisons Traditional beef scheme;
http://www.google.co.uk/search?hl=en&q=morrisons+traditional+beef+scheme&meta=.
Accessed 2/4/2013.

Mrode, R.A. 2005. Linear models for the prediction of animal breeding value. 2nd edition. CABI publishing, Wallingford, UK.

Newman S, Reverter A and Johnston DJ 2002. Purebred-crossbred performance and genetic evaluation of postweaning growth and carcass traits in Bos indicus x Bos Taurus crosses in Australia. Journal of Animal Science 80, 1801-1808.

Nirea KG, Sonesson AK, Woolliams JA, Meuwissen TH.2012. Strategies for implementing genomic selection in family-based aquaculture breeding schemes: double haploid sib test populations.Genet Sel Evol. 2012 Oct 30;44:30. doi: 10.1186/1297-9686-44-30.

Nunez-Dominguez R, Van Vleck LD, Boldman KG and Cundiff LV 1993. Correlations for genetic expressions for growth of calves of Hereford and Angus dams using a multivariate animal model. Journal of Animal Science 71, 2330-2340.

OFT (Office of Fair Trading) 2004. Anticipated acquisition by Genus plc of Supersires. Fleetbank House, London, UK.

Ozkutuk. K. and Bichard, M. 1977. Studies of pedigree Hereford cattle breeding. Animal Production, 24; 1-13.

Pabiou T 2012. Genetics of carcass composition in Irish cattle exploiting carcass video image analysis. PhD, Swedish University of Agricultural Sciences, Uppsala.

Penny CD, Faulkner G, Boreland J, Doyle B, Wilson A, Gibson D and Ballard D 2001. A survey of longevity and reasons for culling in UK beef stock bulls. Cattle Practice 9, 55.

Philip Leat, Cesar Revoredo-Giha, (2008) "Building collaborative agri-food supply chains: The challenge of relationship development in the Scottish red meat chain", British Food Journal, Vol. 110 Iss: 4/5, pp.395 – 411

Phocas, F. and Sapa, J. 2004. Genetic parameters for growth, reproductive performance, calving ease and suckling performance in beef cattle heifers. Animal Science, 79: 41-48.
Pimentel EC, König S. 2011. Genomic selection for the improvement of meat quality in beef. Journal of Animal Science, 90(10):3418-26.

Pollott, G.E. and Stone, D.G. 2006. The breeding structure of the British sheep industry in 2003. DEFRA. London.

Powell, R.L., Norman, H.D. and Sanders, A.H. 2003. Progeny testing and selection intensity for Holstein Bulls in different countries. Journal of Dairy Science, 86; 3386-3393.

Pullar, D. 1998. Breeding strategies for heifer replacements for the suckler herd. Cattle Practice 6, 165-168**.**

Rauw W. M., Kanis E., Noordhuizen-Stassen E. N., Grommers F. J.1998. Undesirable side effects of selection for high production efficiency in farm animals: A review. Livestock Production Science, 56:15–33.

Riddell, I. 2005. Single farm payment: Impact on the UK beef industry. Cattle practice 13(1), 41-44.

Robertson, A. and Asker, A.A. 1951. The genetic history and breed structure of British Friesian Cattle. Empire Journal of Experimental Agriculture 74, 113-130.

Roughsedge T, Lowman B, Amer PR and Simm G 2003. Impacts of alternative replacement breeding systems on biological and economic performance in beef suckler production using a herd level bio-economic model. Animals Science 77, 417-427.

Roughsedge, T., Amer, P.R, Thompson, R. and Simm, G. 2005a. Development of a maternal breeding goal and tools to select for this goal in UK beef production. Animal Science, 81:221-232.

Roughsedge, T., Amer, P. R., Thompson, R., and Simm, G. 2005b. Genetic parameters for a maternal breeding goal in beef production. Journal of Animal Science, 83; 2319-2329.

S. C. Bishop. 2012. Possibilities to breed for resistance to nematode parasite infections in small ruminants in tropical production systems. Animal, (6) Special Issue 05; 741-747.

SAC (Scottish Agricultural College). 2008. Farm management handbook. SAC, Edinburgh, UK.

SAC (Scottish Agricultural College). 2009. Farm management handbook. SAC, Edinburgh, UK.

Sawalha, R.M., Navajas, E.A., Duthie, C., Roehe, R. and Roughsedge, T.R. 2010. 2010. Selection response in UK sheep breeding program with the application of production efficiency traits. Proceeding of the 9th World Congress on Genetics Applied to Livestock Production.

Schaeffer, L.R. 2006. Strategy for applying genome-wide selection in dairy cattle. Journal of Animal Breeding and Genetics. 2006 Aug;123(4):218-23.

Sellick, G. S., Pitchford, W. S., Morris, C. A., Cullen, N. G., Crawford, A. M., Raadsma, H. W., Bottema, C. D. K. 2007. Effect of myostatin F94L on carcass yield in cattle. Animal Genetics, 38:5, 440-446.

Signet Breeding (Division of MLC). 2012. Texel genetic trends and selection indices. Retrieved November 1 2012 from http://www.signetfbc.co.uk/2012 TI

Simm, G. 1998. Genetic Improvement of cattle and sheep. Farming Press, Ipswich, UK.

Simm,G., Bünger,L., Villanueva,B., Hill,W.G., 2004. Limits to yield of farm species: genetic improvement of livestock. In: Yields of Farmed Species: Constraints and Opportunities in the 21st Century, pp. 143-165. Thrompton, Nottingham, UK.

Smith, C. 1984. Rates of genetic change in farm livestock. Research and Development in Agriculture, 1, 79–85.

Solberg, T.R, Sonesson, A.K., Woolliams, J.A. and Meuwissen, T.H.E. 2008. Genomic selection using different marker types and densities. Journal of Animal Science, 86(10):2447-54.

Southgate JR, Cook GL and Kempster AJ 1982. A comparison of different breeds and crosses from the suckler herd. Animal Production 35, 87-98.

Telford, D.J., Beard, A.P. and Franks, J.R. 2003. The potential adoption and use of sexed semen in UK suckler beef production. Livestock Production Science, 84; 39–51.

Tenesa, A., Navarro, P., Hayes, B.J., Duffy, D.L. and Clarke, G.M. (2007). Recent human effective population size estimated from linkage disequilibrium. Genome Resources, 17: 520–526.

The Bovine HapMap Consortium, 2009. Genome-wide survey of SNP variation uncovers the genetic structure of cattle breeds. Science, 324: 528.

Tim Roughsedge, Rainer Roehe, Elly Navajas, Rami Sawalha, Carol-Anne Duthie, Peter Amer, Jorit Nühs, Wagdy Mekkawy, Eileen Wall, Georgios Banos, Geoff Simm. 2010. Determining strategies for delivering environmentally sustainable production in the UK ruminant industry through genetic improvement SAC report for Defra, SAC, Edinburgh, UK.

Todd, D.L. 2007. A survey of the longevity and reasons for disposal of breeding bulls in the Northern Ireland suckler herd. BSc, University of Wales, Aberystwyth.

Toosi, A., Fernando, R.L and Dekkers, J.C.M. 2009. Genomic selection in admixed and crossbred populations. Journal of Animal Science, 88: 32-46.

Van der Werf J.H. J. (2009) Proceedings of the Association of Advancement in Animal Breeding and Genetics, 18:38.

Van Eenennaam, A.L., LI, J., Thallman, R.M., Quaas, R.L., Dikeman, M.E., Gill, C.A., Franke, D.E. and Thomas, M.G. 2010**.** Validation of commercial DNA tests for quantitative beef quality traits. Journal of Animal Science, 85: 891-900.

Van Eenennaam AL, van der Werf JHJ and Goddard ME 2011. The value of using DNA markers for beef bull selection in the seedstock sector. Journal of Animal Science 89, 307-320.

Van Eenennaam, A.L. and Drake, D.J. 2012. Where in the beef-cattle supply chain might DNA tests generate value? Australian Journal of Animal Production Science, 52; 185-196.

Van Grevenhof EM, Van Arendonk JA, Bijma P. 2012. Response to genomic selection: the Bulmer effect and the potential of genomic selection when the number of phenotypic records is limiting. Genetics Selection Evolution. 2012 3;44:26.

Villanueva B., Pong-Wong R., Woollliams J.A. 2002. Marker assisted selection with optimized contribution of candidates to selection. Genetics Selection Evolution, 34: 679–703.

Wiener, G. 1953. Breed Structure in the pedigree Ayrshire cattle population in Great Britain. Journal of Agricultural Science, 43; 123-130.

Wiggans GR, Van Raden PM and Cooper TA 2011. The genomic evaluation system in the United Sates: Past, present, future. Journal of Dairy Science 94, 3202-3211.

Appendix A;

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Gene flow in a national cross-breeding beef population

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Future progress in genetic improvement and the monitoring of genetic resources in beef cattle requires a detailed understanding of the population under selection. This study examines the gene flow in the UK beef population with an uncommon breeding structure involving interaction between the beef and dairy populations. British Cattle Movement Service records were used as the primary source of information, and these data were triangulated with UK government statistics, other industry information sources and existing literature to build up a profile of the UK beef industry. Estimates were made of the breed composition of suckler cows, breeding bulls and the prime slaughter population. Cross-bred animals made up 85% and 94%, respectively, of the commercial beef breeding cow and prime slaughter populations. Holstein/Friesian (through cross-breeding) made up the largest proportion of genes in both these populations with 33% and 28%, respectively. The next five most popular breeds were specialist beef breeds: Limousin (22% and 18%), Charolais (11% and 6%), Simmental (9% and 11%), Angus (7% and 8%) and Belgian Blue (6% and 6%). Combined, the top seven beef breeds accounted for 94% of beef genetics in the prime slaughter population, and 80% of this came from non-native breeds. The influence of dairy breeds in the commercial beef breeding population was highlighted by the fact that 44% of replacement commercial beef breeding females were sourced from beef-sired crosses in the dairy herd, and in total 74% of all maternal grand dams of prime slaughter animals were Holstein/Friesian. The use of selection index technology was also investigated by analysing breeding bull sale results, with the correlation between the terminal sire index and sale price of young breeding bulls being generally moderate but significant, ranging from 0.21 to 0.38 across the major beef breeds. The most influential source of genetics in the commercial suckler beef herd was natural service breeding bulls. These were mostly sourced from pedigree breeders, and accounted for 47.8% of the genetics in the prime beef population. Artificial insemination sires were responsible for 16.6% of prime beef genetics, with the remaining 35.6% coming from dairy breeds, 95% of which was Holstein/Friesian.

Keywords: animal breeding, beef cattle, breeds, gene flow

Implications

An accurate profile of a livestock breeding sector is important in informing decision making regarding the potential for adoption of new genetic technologies and the monitoring of genetic resources. The structure described in this study provides previously unknown data for use in modelling the effects of, for example, the implementation of genomic selection in the UK beef breeding industry. This paper also suggests a protocol for interpretation of existing cattle information sources and proposes adjustments to the national cattle recording database to further increase its value as a research and monitoring tool.

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Introduction

The United Kingdom has a long-standing tradition of beef breeding. Once considered 'the stock yard of the world' (Gibbs *et al.*, 2009) and a leading exporter of seedstock cattle during the first half of the 20th century (Hall and Clutton-Brock, 1989), the UK's beef breeding sector has recently undergone much upheaval. Serious disease epidemics such as bovine spongiform encephalopathy (BSE), volatile meat prices and the introduction of the single farm payment have made for a turbulent period for British beef cattle breeders (Lowman, 1998; Riddell, 2005). On the positive side, the 1990s also saw the introduction of bet linear unbiased prediction (BLUP)-based genetic evaluation, which has given breeders a powerful and objective tool to aid genetic improvement (Amer *et al.*, 1998). Correspondingly, the rate of genetic gain in key traits has seen an increase since the implementation of BLUP

(Amer *et al*., 2007). Nevertheless, in 2010, beef production remains a secondary enterprise on many farm holdings (Lowman, 1998; Defra, 2008a), with an average herd size of just 28, and profitability is largely dependant on subsidy support (Riddell, 2005; Defra, 2008b).

The UK beef industry now has the possibility of implementing new technologies in cattle breeding, such as genomic selection, which could have the potential to increase the commercial viability of the sector (Bishop and Woolliams, 2004). Investigating the breeding structure of the industry is therefore an important part of evaluating the possible merits of such new breeding tools in a UK context.

Pedigree breeding

Elite beef cattle breeding in the United Kingdom has historically been the domain of pedigree breeders, who registered cattle within the appropriate breed herdbooks. This breeding model has remained relatively constant over time, with a small number of 'bull breeding' herds driving much of the selection within particular breeds (Ozkutuk and Bichard, 1977; Allen, 1990). Artificial insemination (AI) has more recently facilitated the wider dissemination of genes from the most popular bulls within these herds (Keeble, 2004).

In contrast, breed use has changed dramatically in recent decades. The 1960s and 1970s saw the importation of European beef breeds such as Charolais, Limousin and Simmental (Hall and Clutton-Brock, 1989). Up until then, only native British beef breeds were in use. In 1968/1969, Hereford and Aberdeen Angus bulls accounted for 61% and 18%, respectively, of beef breeding bull licenses issued by the Ministry of Agriculture (a practice no longer undertaken), with the Charolais (the only non-native breed in use) accounting for less than 1% of bull licenses at this time (Craven and Kilkenny, 1976). These breeds were targeted in the search for new genetics that could produce faster-growing and later-maturing cattle, in order to meet consumer demand for leaner beef (Allen, 1990); their introduction effectively constituted the onset of an industry-wide breed substitution event. Their importation was subject to the formation of UK herdbooks, and thus these new breeds were assimilated into the traditional breeding framework (Edwards *et al*., 1966; MAFF, 1977). Such was their popularity that, by the 1980s, they had largely usurped the traditional British breeds in UK beef production systems (Allen, 1990; Meat and Livestock Corporation (MLC), 1990; Pullar, 1998).

Commercial cross-breeding

Bulls from pedigree herds have traditionally been used to mate with cross-bred 'suckler' females (Lowman, 1997) to produce slaughter animals. Suckler females are those that rear their calf through to weaning, compared with dairy cows that have their calf removed within 48 h for artificial rearing.

The UK suckler herd has, by international standards, an uncommon breeding structure, with large numbers of replacement suckler females sourced from beef cross-breds born in dairy herds (Lowman, 1997). These cross-breds are mostly a by-product of dairy farmers making matings in excess of replacement needs to beef bulls in order to increase the value of by-product calves (Southgate *et al*., 1982; Simm, 1998). This beef × dairy mating strategy was seen as a complementary mating of a dairy cow with reasonable beefing qualities to a more specialised beef terminal sire (Southgate *et al*., 1982). Thus, the adoption of cross-breeding in the suckler herd was born as much by opportunism over the availability of dairy cross-breds with advantageous additive genetic qualities as any particular drive to impart hybrid vigour into suckler beef breeding systems (Lowman, B.G., personal communication, 2010). The quantitative map of the gene flow of genetics from the dairy herd into the beef herd is summarised in Figure 1 (this figure also contains results that will be discussed later in the paper), demonstrating the interplay between the dairy and beef herds in UK prime beef production. Throughout the following text, genetic groups such as beef, dairy and their crosses will make use of abbreviations B, D and combinations such as B × D. Here B × D refers to an animal that has a beef sire and a dairy maternal grand sire (MGS) and other crosses are defined analogously. In this context, the suckler herd is defined as a B × B and B × D breeding females, and the dairy herd as D × D breeding females.

Prime beef

The main aim of the UK beef industry is to produce the 'prime' animal. Traditionally, this referred to an animal slaughtered at approximately less than 3 years of age. However, the UK BSE epidemic of the 1990s saw the introduction of a specific age at slaughter restriction of 30 months or less, with meat from cattle aged over 30 months at slaughter banned from entering the human food chain between 1996 and 2006 (Defra, 2006). The prime animal thus became rigidly defined as one aged up to 30 months of age at slaughter. Even after the removal of over 30-month restrictions, a significant market premium remains for carcasses from under 31-month cattle.

Genetic evaluation

In the absence of dedicated large-scale beef cattle breeding companies, a partnership between breed societies and MLC/Signet facilitated the implementation of a BLUP-based genetic evaluation in pedigree herds. Agricultural Business Research Institute (ABRI) from Australia now also provides this service to some UK-based breed societies. Genetic links from common ancestors across pedigree herds have allowed the calculation of BLUP-estimated breeding values (EBV) that are comparable across the whole breed. These links were largely achieved through the relatively high use of AI in pedigree herds (compared with commercial suckler herds), which remains at around 25% in the Limousin breed, for example (Keeble, 2004). Selection of terminal sires is driven largely by lean meat yield traits, such as growth rate, muscling and fat depth. Although the Signet Beef Value selection index is a good predictor of grading under the European Union beef carcass classification system (EUROP; Simm, 1998), genetic correlations with calving and maternal traits tend to be negative. Eriksson *et al*. (2004) found higher EUROP carcass conformation to be negatively correlated

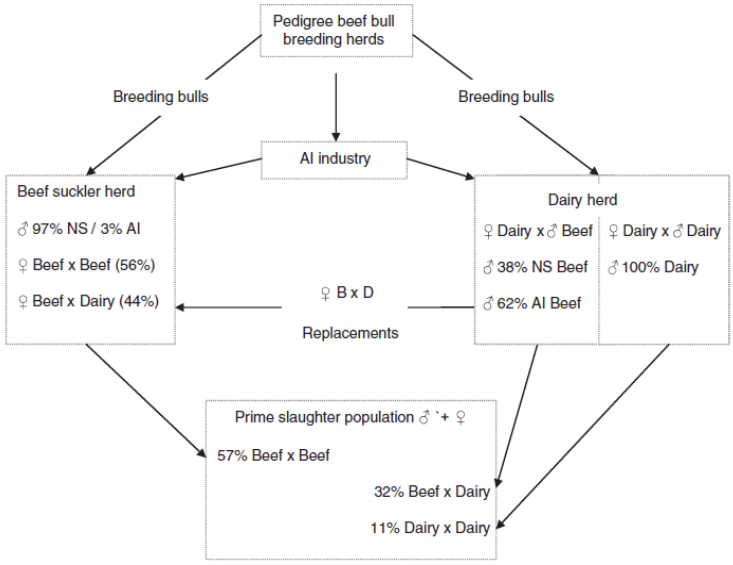

Figure 1 Overview of the gene flow in the UK beef population highlighting proportions of natural service (NS) and artificial insemination (AI), as well as proportions of beef (B) × dairy (D) suckler females, and proportions of beef and dairy in the prime slaughter population (based on sire and maternal grandsire from 2007/2008 British Cattle Movement Service/Scottish Agricultural College).

with calving ease, whereas Roughsedge *et al.* (2005) found that higher 400-day weight was negatively correlated with age at first calving.

Furthermore, every major UK beef breed has seen a deterioration in genetic trends for calving ease since evaluation of this trait was first introduced in 1997 (BASCO, 2010; Breedplan, 2010). This evidence for terminal and maternal/calving selection goals being antagonistic in beef cattle breeding makes selection for dual-purpose goals more problematic without careful use of economic selection index methodology. Therefore, the preferential selection for terminal beef traits has seen deterioration in calving traits in all recorded pedigree beef breeds. In order to address this issue, certain breeds have incorporated calving traits into global selection indices. The genetic gain in growth and carcass traits has, however, been modest in comparison with other livestock species with more intensive production systems (Simm *et al.*, 2004).

Although the introduction of EBV technology in the United Kingdom in the mid-1990s has seen an improvement in the rate of gain in certain traits in elite pedigree populations, there has been no objective study on the influence of improved genetics on commercial bull-buying decisions.

The combination of a somewhat marginalised, economically volatile sector with a traditional structure is also reflected in the low volume of research that has taken place, resulting in relatively poor knowledge of basic industry statistics. Application of new technologies such as genomic selection will rely on accurate predictions of potential benefits in order to gain acceptance and funding for their implementation. The uncommon breeding structure described above infers that the pathway to implementation will be different from that of other beef breeding countries. The objective of this study was therefore to produce an extensive profile of the UK's beef breeding sector using existing information sources, in terms of breed composition, genetic resource use and commercial uptake of EBV technology. Such a profile could provide the groundwork for evaluation of the potential benefits of genomic selection.

Method

An important source of data, the British Cattle Movement Service (BCMS), was established in 1996, in the wake of the BSE crisis, to trace cattle births, deaths and movements using CTS (the Cattle Tracing System). In this study, the data were obtained from the Scottish Agricultural College's (SAC) restricted version, which will be referred to as BCMS/SAC in this report. This study used all BCMS/SAC records for cattle in Great Britain (GB; comprising England, Wales and Scotland), whose death was recorded by BCMS between 1996 and 2008 inclusive, and extracted the following data for each animal: UK registration number, sex, year of birth, age at death in months, breed code, dam identification and maternal breed code.

Defra farm surveys and slaughter censuses

Information from Defra censuses and slaughter surveys was used to triangulate with the BCMS/SAC records so as to enable a cross-referenced UK breed composition profile to be established. The Defra cattle census was collated annually

from UK regional agricultural surveys until 2004. After this date, English and Welsh data were obtained from the BCMS records, but Scottish and Northern Irish data continued to be based on their respective agricultural surveys. As such, pre- and post-2004 survey results were not necessarily directly comparable. Furthermore, the level of detail in English and Welsh surveys was reduced; for example, mature bull numbers were omitted, which are important to this study. Therefore, only pre-2004 cattle survey numbers were used in this study.

Reconciliation of BCMS/SAC and Defra farm surveys and slaughter censuses

Owing to the nature of the BCMS/SAC data and the availability of Defra slaughter records, the most reliable starting point for the industry profile was the prime slaughter population, which yielded a relatively representative data set to establish breed proportions. As BCMS/SAC records were of dead animals, the GB slaughter population was completely represented in this data set.

Defra slaughter surveys, compiled monthly from UK slaughterhouses, recorded prime cattle in three categories only – bulls, steers or heifers – and recorded adult cattle in two categories only – cows and bulls. Thus, no breed information was included in these statistics, and in order to establish the genetic make-up of these cattle the BCMS/SAC records were analysed to determine breed composition. As BCMS/SAC covers only GB, and Defra surveys cover the entire United Kingdom, which is GB plus Northern Ireland (NI), and the proportions of beef and dairy cattle differs between GB and NI, an adjustment was necessary to reconcile these data. According to the 2003 Defra census, 50.7% of NI breeding cattle were in the beef herd compared with 43.6% in GB. Given that 15% of the total 2003 UK breeding cattle population was in NI, the UK total beef proportion was 44.6%. The BCMS/SAC proportion of prime cattle with dairy dams was therefore reduced by a factor of 0.98 (43.6/44.6).

A further adjustment to the BCMS/SAC proportion of prime cattle with dairy dams was needed, owing to the fact that a prime animal record including breed of dam would only appear if the dam's death had also been recorded by 2008. BCMS/SAC only included records of animals registered as dead in BCMS and each individual animal record only included the animal identification number of its dam and no other information such as breed code. Therefore, only 755 000 (out of a total of 1.7 million) animals whose dam was also recorded as dead in BCMS were included in the prime slaughter analysis. It was therefore important to adjust any bias in this sample, which could have led to an overrepresentation of a particular breed or group of breeds. Given that the most critical longevity differences are between cows producing in dairy or beef herds, rather than between breeds in the beef herd, there was a need for adjustment between beef and dairy but not between individual beef breeds. This was achieved by a further search of BCMS/SAC, identifying the subset of records that included the dam. These records were scaled to the Defra slaughter totals, using BCMS/SAC to provide breed proportions, and to estimate the number of prime cattle originating from the national beef and dairy herds, respectively. A conditional probability calculation, using animals registered as dead in 2008 at in BCMS/SAC, showed that dairy breed-coded females of calving age were 1.29 times as likely to be dead within the lifespan of an average prime animal as beef breed-coded females of calving age (see Appendix 1). The proportion of prime cattle records with dairy dams was reduced accordingly.

Interpretation of breed coding in BCMS

For the purposes of this study, it was assumed that an animal's breed code, as it appeared in BCMS/SAC, referred to the breed of its sire. The Cattle Book (Defra, 2008b), for example, describes the cattle breed field in BCMS as 'usually based on the breed of sire'. However, this protocol was not explicitly stated in BCMS literature (Cattle Keepers Handbook, 2009). If the animals' breed code contained an X (denoting a cross-breed), it was assumed that this referred to the animal itself being cross-bred, rather than its sire. Therefore, an LIMX-coded animal was presumed to be the product of the mating between a pure-bred Limousin bull and any dam other than a pure-bred Limousin. Breed coding was inconsistent before 2000, and to a lesser extent post 2000, in BCMS. For example, Limousin cattle appear to have been coded in six different ways (excluding crosses) up until 2000 (Lim, Lm, Li, L, LimB and LimR). As such, pure-breed numbers in pre-2000-born animals in this study reflect the amalgamation of such codes for each breed. As this was primarily a beef breed study, all Holstein or Friesian cattle (and variants such as British Friesian) were classed as Holstein/Friesian. It was also assumed that dairy-sired females were not used as suckler cows in the beef breeding herd. Blonde d'Aquitaine and Belgian Blue breed societies have now renamed themselves as British Blonde and British Blue, respectively. For the purposes of this paper, the original names will be used as the majority of animals of these breeds in the data set were born before these changes.

Breed codes were also not necessarily a good indicator of pure- or cross-bred status. For instance, only 38% of animals coded AA (Angus pure-breed code) in the data born since 2000 and dead by 2008 actually had dams coded AA; 11% were coded AAX (Angus cross-breed code) with 51% of dams having a variety of other (non-angus) breed codes. This was not an issue exclusive to AA, with only 43% of animals coded CH having dams also coded CH, 8% coded CHX and the remaining having a variety of other codes. This coding pattern confirms the assertion that animals are coded by sire breed rather than the breed make-up of the animal itself.

The approximate genetic make-up of animals was therefore calculated by using their sire and MGS breed codes. These sires were assumed to be pure-bred, as per the literature (Penny *et al.*, 2001; Todd, 2007). For example, an animal coded CH or CHX, with a dam coded LIM or LIMX was interpreted as being 50% Charolais and 25% Limousin, with the other 25% unknown. This remaining 25%, effectively the genetic make-up of the maternal grand dam (MGD), could

not be calculated from BCMS/SAC because of very low numbers of animal records in BCMS/SAC with maternal great grand sire breed codes. In summary, BCMS/SAC provided an extensive profile of the sire and MGS breeds for the prime slaughter and adult breeding populations, constituting 75% of the animal's genetic make-up. To overcome this problem, the remaining 25% was estimated according to Appendix 2, which calculated the overall proportion of beef and dairy genetics in the respective populations.

Suckler cows

In estimating the breed proportions of suckler cows, no correction was made for survival of dairy-sired dams being less than beef-sired dams. Although Appendix 1 did show that beef dams live longer than their dairy counterparts, the average lifespan of the progeny in this case (the suckler cow) was much older (98 months in 2007 BCMS/SAC) and the pattern of death suggested that it was not necessary to correct for dairy dam survival.

The most common suckler cow genotypes (in terms of the animal and its dam's breed codes) were estimated from females with a beef sire aged over 30 months at death in 2007 in BCMS/SAC. No edit was carried out regarding pure-bred (and potentially pedigree) females as these could not be reliably separated in the data set, but will make up less than 5% of cows defined in this way. Again, similar breed codes were combined, including cross-breed codes (e.g. a LIMX × AAX was categorised with LIM × AA and referred to as a Limousin cross Angus). This search again yielded a reduced data sample in BCMS/SAC, with the same issue as in the prime slaughter animal study of the dam having to be recorded as dead in BCMS/SAC for the animal's record to appear. The assumption nevertheless was that this would still be a representative sample of suckler cows in 2007. These results were scaled to the beef breeding female population estimate from the 2006 Defra survey of 1.9 million head.

AI and NS (natural service)

Estimating the numbers of AI-sired animals in the beef and dairy herds was achieved using information from a commercial AI company (Genus PLC) and a UK Office of Fair Trading (OFT) report (Genus PLC, Crewe, UK, personal communication; OFT, 2004). OFT estimated that 3% of females in the beef herd were bred to AI. Given that the 2008 B × B prime slaughter population numbers 1.16 million (Table 1), around 35 000 of these would therefore have been AI sired, assuming that 1 calf is born from every 2.5 straws of semen sold (Genus PLC, Crewe, UK, personal communication). This would have required approximately 90 000 straws of beef semen, and from the total estimated annual beef semen market in the United Kingdom of 1.1 million straws this would have left 1 010 000 straws for use in the dairy, resulting in 404 000 beef AI-sired calves in that sector.

NS breeding bull numbers and breed proportions were estimated from a combination of: the Defra slaughter census, Defra farm surveys, AI statistics and BCMS/SAC males aged over 47 months at death, with identical sire and MGS breed codes (e.g. CH animal and CH dam or SM animal and SM dam). All cross-breds (23% of records) were removed from the data, as it was considered that the proportion of cross-bred breeding males in the national cattle herd was less than 1% (Penny *et al.*, 2001; Todd, 2007). The over 47 months criteria, rather than over 30 months, were used to estimate breed proportions, because of the phenomenon of a small percentage of animals intended for beef (almost certainly male castrates) being culled at over 30 months of age, probably in error rather than by design. Although these over 30-month culls represent a small proportion of prime culls, they are enough to confound the relatively small numbers of adult breeding bulls dying each year. To triangulate and provide additional information, these BCMS/SAC over 47-month breed proportions were also compared with BCMS annual registration data (published for the top five breeds by the British Limousin Cattle Society, BLCS) and estimates of AI-sired calves from industry statistics (Genus PLC, personal communication) to estimate total breeding bull numbers according to varying cow to bull mating ratios. Estimating numbers of breeding bulls aged under 31 months at death was not feasible using BCMS/SAC, given that not all males with identical sire and MGS pure-breed codes would necessarily have been destined for breeding purposes. As mentioned above, in order to estimate breeding bull numbers, a survival probability was calculated from bulls aged over 30 months at death, from the top seven beef breeds with deaths recorded in 2008. This provided a lifespan pattern for breeding bulls with which to estimate the numbers of bulls alive in the population at any one time, and importantly the numbers entering service annually. The survival probabilities for breeding bulls aged between 18 and 42 months were obtained from McGowan (2006) and Todd (2007), as breeding bulls and male castrates in this age range could not be reliably separated in BCMS/SAC.

Pedigree

In order to establish whether potential breeding males within BCMS/SAC were pedigree, the BCMS records of Belgian Blue, Charolais and Limousin males were cross-checked against information in the publically accessible genetic evaluation databases, BASCO and Breedplan. Estimates of pedigree cattle numbers were based on records of cattle born after 2000, because in 2000 all UK registration numbers were standardised and changed to a numeric format (BCMS, 2009). Cross-referencing registration numbers of cattle born before 2000 was found to be unreliable because of differences in formatting between BCMS and BASCO/Breedplan records, as well as inconsistency in formatting within BCMS itself.

Relationship between sale prices and terminal selection index of breeding bulls

As an indication of the use of selection indices by bull buyers, the sale price of pedigree bulls of the four top breeds numerically sold at official 2009/2010 breed sales was correlated with the Limousin Beef Value index (for Limousin) and the Terminal Sire Index for Angus, Charolais and Simmental.

Table 1 *The 2008 prime slaughter population, categorized by beef (B) or dairy (D) type*

	B × B ♂	B × D ♂	D × D ♂	B × B ♀	B × D ♀	D × D ♀	Total B × B	Total × D
GB proportions[a]	0.28	0.22	0.10	0.22	0.16	0.02		
UK proportions[b]	0.32	0.19	0.09	0.25	0.13	0.02	0.57	0.43
UK totals (000s)	647	378	183	513	272	36	1160	869

GB = Great Britain; BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College.
B×B ♂ represent males with a beef breed sire and a beef breed maternal grand sire.
D×D ♀ represent females with a dairy sire and a dairy maternal grand sire.
Prime animals were defined as those aged between 10 and 30 months inclusive at death.
[a]Unadjusted 2008 BCMS/SAC data.
[b]2008 BCMS/SAC data adjusted for Northern Ireland and dairy dams.

Results and discussion

Prime slaughter population

In total, 2 018 563 cattle aged under 31 months at death were recorded as having died in Great Britain in 2008 BCMS/SAC. Of these, 89% or 1.80 million died between 10 and 30 months of age, reflective of prime slaughter ages. This compares with 1.72 million animals in the collated Defra GB slaughter statistics for 2008, which is 4.3% lower and consistent with expected mortality levels in beef rearing systems (SAC, 2009), as slaughter statistics do not include on-farm deaths. Given that Defra slaughter statistics suggests that 18% of the total UK prime slaughter cattle are born in NI, scaling for this, the estimated UK prime slaughter population total would have been 2.12 million (2 018 563 × 0.89 × 1.18).

Table 1 shows a breakdown of this 2008 prime slaughter population by herd of origin. Here, beef × beef animals were born in the suckler herd, whereas beef × dairy and dairy × dairy were born in the dairy herd. Holstein/Friesian accounted for 95% of dairy breed codes in BCMS/SAC. From this information, the proportions of genetics coming from NS beef bulls, AI beef bulls and dairy bulls in the prime beef population was estimated using Appendix 2. Assuming equal use of NS- and AI-sired beef × dairy replacement females, the relative genetic proportions were estimated as: 47.8% NS beef, 16.6% AI beef and 35.6% dairy. Therefore, the prime slaughter population was composed of 64% beef and 36% dairy genetics.

It should be noted that the proportion of dairy genetics in this population is heavily reliant on the numbers of dairy-sired bull calves actually reared to prime slaughter, given the high rates of slaughter of these calves at birth. Typically, only 50% of dairy-sired calves have been reared beyond birth in the last 5 years (Beyond Calf Exports Stakeholders, 2010).

Prime breed composition

Recently imported European breeds contribute the majority (around 50.5%) of all the genetics in this prime slaughter population, with 'native' British breeds contributing less than 14% (Table 2). Limousin is the most influential beef breed in the United Kingdom with just over a fifth of the genetic contribution to the prime slaughter population. The top seven beef breeds include two British breeds and combined account for 61% of the total genetics and 94% of the beef contribution. These are the only breeds that are used on a nationwide basis in the United Kingdom, and are also those beef breeds with significant sales for UK AI companies (Genus PLC, 2010, personal communication). The relative use of the most popular beef sire breeds in the beef and dairy sectors is shown in Table 3, with Limousin, Belgian Blue and Angus being equally popular across beef and dairy herds. Charolais, by contrast, is much more heavily used in the beef herd.

Table 2 *Breed genetic contribution to the 2008 prime slaughter population*

Breed	Breed code	Sire[a]	MGS[a]	Remainder[b]	Total
Limousin	LIM	15.5	4.6	1.7	21.8
Charolais	CH	9.3	1.3	0.5	11.1
Simmental	SM	5.2	2.6	1.0	8.8
Belgian Blue	BB	4.5	1.0	0.4	5.9
Blonde	BA	1.8	0.4	0.1	2.3
Other imported beef		0.4	0.2	<0.1	0.6
Total imported beef					50.5
Holstein/Friesian	HF	4.5	9.7	18.4	32.6
Native dairy		0.1	0.3	1.2	1.6
Other imported dairy		0.3	0.3	1.2	1.8
Total Dairy					36.0
Aberdeen Angus	AA	4.4	1.9	0.7	7.0
Hereford	HE	1.9	1.3	0.5	3.7
South Devon	SD	0.6	0.3	0.1	1.0
Welsh Black	WB	0.3	0.2	0.1	0.6
Devon	DEV	0.2	0.1	<0.1	0.3
Galloway	GA	0.1	0.1	<0.1	0.2
Highland	HI	0.1	0.1	<0.1	0.2
Other native beef		0.3	0.2	<0.1	0.5
Total native beef					13.5
Total		50	25	25	100

BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College; MGD = maternal grand dam; MGS = maternal grand sire.
[a]Figures calculated from BCMS/SAC. Contributions were adjusted according to beef or dairy dam survival probability.
[b]Estimated remaining 25% of genes, made up of the MGD. This could not be calculated from BCMS/SAC. The Holstein/Friesian proportion was therefore estimated according to Appendix 2, which calculated that 36% of the genes in this population were from dairy breeds, and that Holstein/Friesian makes up 95% of the dairy contribution. The remaining MGD contribution was then assigned pro rata to the beef breeds as per their MGS proportions.

The differences between breed contributions in GB and NI are shown in Table 4, with notably greater use of Charolais in this latter region. However, as shown in Table 4, combining NI with the GB data set only increases the overall sire contribution of Charolais by 2% whilst increasing Simmental and reducing Belgian Blue by 1% each. Therefore, in terms of breed use, BCMS was reasonably representative of the United Kingdom as a whole, and introduced only a small bias. The BCMS annual registration data shown in Table 4 can also be used to assess trends in breed use. Sensitivity over years was tested by extracting 2005, 2006 and 2007 BCMS/SAC data, with no major differences found in breed proportions. Similarly, 2008 BCMS birth registration data suggest only minor changes from 2005, with Limousin, Simmental and Belgian Blue identical and with Charolais 16% (down 2%) and Angus 13% (up 2%), (BLCS, 2006 and 2009).

In the last 40 years, breed use in the UK beef herd has therefore changed dramatically, to the extent that around 75% of beef genes in the prime slaughter population are non-native. The Aberdeen Angus is the one native breed to have maintained a significant market share of beef genetics, in comparison with 1970s bull license data (Craven and Kilkenny, 1976), yet even the influence of this breed has halved within the above timescale.

Table 3 *A comparison of the beef breed sire use (natural service plus artificial insemination) in beef and dairy herds (estimated from the 2008 prime slaughter population)*

Breed	% beef herd	% dairy herd
Limousin	35	31
Charolais	20	8
Simmental	12	20
Belgian Blue	10	11
Angus	11	14
Others	12	16
Total	100	100

Table 4 *Births registered by beef sire breed in 2005 in BCMS (Great Britain) and APHIS (Northern Ireland) reproduced the 2006 BLCS studbook and factfinder (BLCS, 2006; '000s)*

Sire breed	BCMS	%	APHIS[a]	%	Total	%
Limousin	709	35	134	34	843	35
Charolais	358	18	115	29	473	20
Simmental	232	11	20	5	252	10
Angus	216	11	42	11	258	11
Belgian Blue	194	10	33	8	227	9
Others	308	15	55	14	363	15
Total	2017	100	399	100	2416	100

BCMS = British Cattle Movement Service; APHIS = Animal and Public Health Information System; BLCS = British Limousin Cattle Society.
[a]APHIS is the Northern Ireland equivalent of the Cattle Tracing Scheme.

Suckler female population

Overall estimates of the total UK female breeding herd in 2006 were provided by Defra census information. These suggested that there were 1.9 million beef females (cows plus in calf heifers) and 2.4 million dairy females (cows plus in calf heifers). The estimated numbers of B × B males and females slaughtered (Table 1) indicated that approximately 134 000 (647 000 minus 513 000) females were retained within the suckler herd for breeding in 2008. Similarly, the numbers of B × D males and females suggested that 106 000 beef-sired females from the dairy herd were kept as replacement suckler cows in 2008. Therefore, 44% of replacement suckler breeding females came from the dairy herd in 2008.

Breed composition of suckler females

Females retained within the suckler herd per breed of sire are shown in Table 5, with 94% of these sired by the top seven breeds identified previously. The breed contributions to replacement suckler females (Table 6) show a similar pattern to the prime slaughter animals, with slightly more Angus and Hereford influence. Commonly regarded as the most extreme terminal beef breed, the Belgian Blue actually has similar contributions to both prime slaughter and replacements. In contrast, the Charolais influence is halved in the suckler female group. This is reflective of the high use of Belgian Blue AI in the dairy herd, and consequent availability of Belgian Blue × dairy females, as well as the positive contribution to

Table 5 *Estimated numbers of females retained for suckler breeding, by sire breed from the 2008 prime slaughter population in BCMS/SAC, percentages retained of each sire breed and of total females*

Sire breed	Males	Females	Retained[a]	% of sire breed retained	% of total females retained
Limousin	305 151	242 532	62 619	21	31
Angus	101 405	66 561	34 844	34	17
Simmental	98 720	66 699	32 021	32	16
Belgian Blue	82 770	57 536	25 234	30	12
Hereford	42 908	26 203	16 705	39	8
Charolais	152 134	135 783	16 351	11	8
Blonde	34 006	29 979	4027	12	2
Others	52 155	39 912	12 243	–	6
Total	869 249	665 205	204 044	–	100

BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College.
[a]Retained = males minus females and assumes a 50 : 50 ratio of males to females reared to slaughter age.

Table 6 *Breed genetic contributions to the 2007 suckler female population*

Breed	Sire[b]	MGS[b]	Remainder[c]	Total (%)
Limousin	14.2	3.0	0.8	18.0
Charolais	4.5	1.4	0.3	6.2
Simmental	7.1	3.4	0.9	11.4
Angus	6.3	1.6	0.4	8.3
Belgian Blue	4.7	0.7	0.2	5.5
Hereford	3.7	1.1	0.3	5.2
Blonde	1.4	0.3	0.1	1.9
Holstein/Friesian[a]	–	10.3	18.0	28.2
Others	8.0	3.3	4.2	15.5
Total	50	25	25	100.0

MGS = maternal grand sire; BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College; MGD = maternal grand dam.
[a]It was assumed that no Holstein/Friesian sired (or other dairy breed) females were used as suckler cows.
[b]Figures calculated from beef-sired females aged >30 months at death in 2007 BCMS/SAC.
[c]Estimated remaining 25% of genes, made up of the MGDs which could not be calculated from BCMS/SAC. The Holstein/Friesian proportion was therefore estimated according to Appendix 2, which calculated that 29.7% of the genes in this population were from dairy breeds, and that Holstein/Friesian makes up 95% of the dairy contribution. The remaining MGD contribution was then assigned pro rata to the beef breeds as per their MGS proportions.

Table 7 *The 10 most common suckler cow genotypes in the United Kingdom estimated from 2007 BCMS/SAC*

Sire	MGS	%	Number of females ('000s)
Limousin	Holstein/Friesian	10.7	203
Limousin	Limousin	8.1	153
Simmental	Simmental	6.0	114
Belgian Blue	Holstein/Friesian	5.9	111
Hereford	Holstein/Friesian	5.3	101
Angus	Holstein/Friesian	4.5	85
Simmental	Holstein/Friesian	4.4	84
Angus	Angus	3.6	68
Charolais	Charolais	3.4	65
Limousin	Simmental	2.9	55
Total (top 10)		54.8	1039

BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College; MGS = maternal grand sire.

suckler carcass traits of the Belgian Blue. Indeed, these two breeds were at opposite extremes in terms of their pattern of use, with Belgian Blue being largely an AI breed with relatively low levels of NS, and Charolais being largely an NS breed with low AI use. The 10.3% Holstein/Friesian MGS contribution to suckler females is consistent (10.3/25/0.95 = 43.4%) with approximately 44% of suckler cows being born in the dairy herd in Table 1. Altogether, 94.3% of these 2007 suckler females were cross-bred (as defined by those without two matching sire and grand sire pure-breed codes).

The most popular suckler cow genotypes are shown in Table 7, with a very diverse range of breed combinations present. Interestingly, the two most popular genotype groupings appear to be either first-generation crosses from the dairy herd

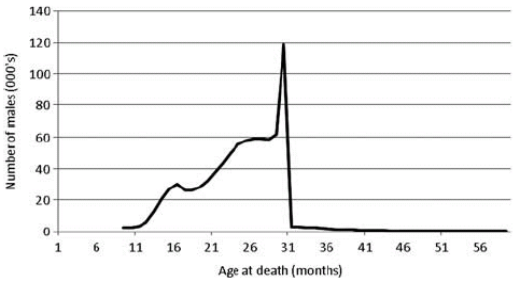

Figure 2 The pattern of male deaths for beef-sired males aged between 8 and 58 months at death inclusive in 2008.

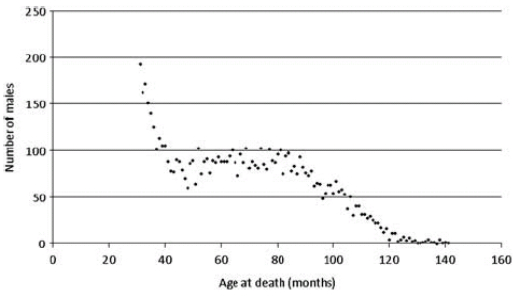

Figure 3 The age at death profile of males aged over 30 months of age at death in 2008 with pure-bred sire and maternal grandsire from the top seven beef breeds.

or 'three-quarter'-bred suckler beef replacements (with the same breed of sire and MGS). Although this table only includes 54% of sucklers, if there was wide-scale rotational cross-breeding in UK suckler herds, it would be expected to feature among the most popular genotypes. However, the most common rotational breed mix, Limousin × Simmental (which was the most common female with different beef breed sire and MGS) breed only accounts for 2.9% of total sucklers.

Breeding bulls

The assumption that very few cross-bred breeding bulls were in use and that cross-bred males aged over 30 months at death were actually castrates is supported by Figure 2, which shows a 'spill over' from the huge drop off in male slaughtering around the 30-month age limit. A more detailed view of male deaths, for animals with identical beef sire and MGD breed codes, in Figure 3, shows a dip in deaths around 47 months before resuming a temporary upward trend, which is consistent with the hypothesis that this profile is a mix of the distributions of slaughter and breeding males.

The 2004 Defra census reported 101 000 total breeding bulls in the United Kingdom (the last year for which this total is available; Defra, 2004). From dairy AI statistics (Genus PLC, personal communication), it was estimated that there were around 200 000 NS dairy calves in 2005. Assuming a conservative mating ratio of 20 calves per bull would

Table 8 *Numbers of beef-sired calves born in 2006 by AI and NS, and NS sires required to father them and estimated number of bulls in BCMS/SAC aged over 47 months at death (BLCS, 2006; 000's)*

	UK calves registered in 2005			Numbers of NS sires required			
Breed of sire	Total	AI sired	NS sired	At 20 calves/sire	At 25 calves/sire	At 30 calves/sire	BCMS/SAC <47 month bulls[a]
Limousin	843	150	697	34.9	27.9	23.2	26.4
Charolais	473	16	457	22.9	18.3	15.2	18.2
Simmental	252	17	235	11.8	9.4	7.8	10.9
Angus	258	40	218	10.9	8.7	7.3	11.8
Belgian Blue	227	170	57	2.9	2.3	1.9	3.6
Others	363	11	348	17.4	13.9	11.6	20.0
Total	2416	404	2012	100.8	80.5	67.0	91.0

AI = artificial insemination; NS = natural service; BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College.
[a]This column gives an estimate of the numbers of the NS beef bulls present in 2006 by breed in the national cattle herd from an estimated total of 91 000 bulls in use, using breed proportions from males aged over 47 months at death in 2005 BCMS/SAC.

Table 9 *Age profile of NS beef breeding bulls in use in the national herd in 2006*

Bull age[a] (months)	Survival probability[c]	Total[d]	Limousin	Charolais	Belgian Blue
18[b]	0.90	20 115	5836	4023	796
30[b]	0.89	18 065	5241	3613	715
42	0.82	16 014	4646	3203	634
54	0.77	13 184	3825	2637	522
66	0.70	10 109	2933	2022	400
78	0.57	7033	2041	1407	278
90	0.46	4019	1166	804	159
102	0.28	1845	535	369	73
114	0.20	513	149	103	20
126	0.01	104	30	21	4
Total		91 000	26 402	18 200	3601

NS = natural service; BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College.
[a]Bulls were assumed to enter breeding service in herds at an average age of 18 months.
[b]Numbers in years 1 and 2 have been adjusted to remove castrates according to literature estimates of breeding bull deaths in these years (McGowan, 2006; Todd, 2007).
[c]Survival probability derived from 2008 BCMS/SAC data for bulls aged <30 months at death, and refers to the probability of a bull surviving the following 12 months.
[d]It was assumed that 91 000 bulls were in service in 2006.

suggest that around 10 000 NS dairy bulls were included in the Defra census total. Thus, the estimated NS beef bull population in 2006 was 91 000, and this figure was used in Tables 8 and 9 to further estimate numbers of bulls by breed. Table 8 shows the estimated numbers of NS bulls required to sire the approximate number of NS bred calves born in 2005. Three different calves/bull ratios are shown, depicting likely breeding ratios.

Table 9 uses a survival pattern from beef bulls aged over 30 months at death, from the top seven breeds with two identical sire and MGS pure-breed codes recorded in BCMS/SAC as having died in 2008. The estimated average herd life of these bulls was 4.5 years with only minor between-breed differences. Therefore, assuming a total of 91 000 NS beef breeding bulls total translates to approximately 20 000 breeding bulls entering service each year. This is similar to the study by Amer *et al.* (2007), which estimated 19 346 beef sires purchased by commercial farmers each year. Further support for these estimates comes from Defra slaughter statistics that recorded 17 800 adult bull culls in 2008 and 19 600 in 2009 (Defra, 2010). Survival probabilities for 10 years of service are shown, as well as calculations for three individual breeds. Estimates of breeding bulls entering service each year (row 1) are in reasonable agreement with approximate annual pedigree registrations for 2008. For example, there were approximately 4000 Charolais males registered in 2008 (BCCS, 2009) and approximately 900 Belgian Blue (BBCS, 2009). Limousin registrations were somewhat higher than the figure in Table 9 at approximately 8000 (BLCS, 2009). The pedigree registration of a bull is not a guarantee that it will become a breeding animal. It is also likely that Limousins are popular with breeders maintaining closed beef production systems. Therefore, in the same way that large numbers of Holstein dairy cows are pedigreed without necessarily being elite breeding animals, a similar system may be used in some Limousin herds.

Table 10 *Relationship between sale price and terminal index of young breeding bulls sold at official breed society sales in 2009/2010*

Terminal index range[1]	Limousin	£	Charolais	£	Angus	£	Simmental	£
Top 1%	84	7495	31	6740	23	8845	6	6843
2% to 10%	235	6549	85	6769	79	4564	26	4862
11% to 25%	155	5252	67	6048	33	3400	27	3999
26% to 50%	110	4654	79	5279	9	3540	15	3724
Below median	51	3717	83	4131	5	3633	8	3545
Total bulls	635		345		149		82	
Correlation	0.25		0.21		0.38		0.32	
Regression (£/index point)	160		112		255		181	

[1]Terminal index refers to Limousin Beef Value and Charolais, Angus and Simmental terminal selection indices.

Sire identification

The proportion of prime animals with UK registration number sire identifications (id) included in their BCMS records varied from just 9% of Belgian Blue-sired animals up to 37% of Angus-sired animals, among the top seven beef breeds. The other five of the top seven beef breeds were all in the range between 21% and 28%. Approximately 1% of animals had other sire id variants such as breed, name of sire or tattoo numbers. No individual sire had more than 100 progeny in this data set, suggesting an absence of AI sire recording. As such, BCMS does not provide an unbiased sample of sire identification numbers. The lack of AI sire recording also explains the particularly low figure for Belgian Blue sire id, given that the vast majority of calves from this breed are AI bred (Table 8).

Influence of pedigree breeding

The extent to which the historical practice of registering pure-bred breeding males in pedigree herdbooks still exists was of major interest in characterising the UK breeding industry. This analysis again focused on males aged over 47 months at death as these were seen as the group that could most reliably be interpreted as breeding males. Sampling the first 100 Charolais males by date of birth (with CH sire and MGS breed codes), born in 2000 and aged over 47 months at death in BCMS/SAC, 84% were registered as pedigree males in the ABRI database. Similarly, 90% of the first 100 Belgian Blue coded BB (sire and MGS) males born in 2000 and aged over 47 months at death were recorded in the ABRI database as pedigree. Limousin numbers were slightly lower, with 76% of the first 100 Limousin coded LM (sire and MGS) males born in 2000 and aged over 47 months at death were recorded in the BASCO database as pedigree. These figures constitute a lower estimate given the formatting differences between BCMS and the pedigree databases. Cross-referencing BCMS/SAC with ABRI and BASCO therefore suggested that the majority of animals that could be reasonably expected to be breeding bulls (i.e. aged over 47months at death) were pedigree. It did appear, however, that there may be significant numbers of non-registered pure-bred bulls in use, perhaps as high as 24% in Limousin.

Investigation of males aged just over 30 months of age at death highlighted the problem of males reared for slaughter confounding the identification in BCMS/SAC of breeding males culled early in their reproductive careers. Taking all of the 2002-born Belgian Blue (coded BB; 39) and CH (75) males in BCMS/SAC aged 31 to 33 months at death, 49% of BB and 47% of CH were registered in the ABRI database as being pedigree, or had an imported identification number (suggesting imported breeding bulls). This adds further evidence to the suggestion that males culled at just over 30 months of age are a mixture of beef steers and breeding bulls (see also Figure 3).

Relationship between sale prices and terminal selection indices of breeding bulls

Correlations between sale prices of breeding bulls and terminal selection indices were significant ($P < 0.01$), but of a moderate strength (Table 10). Terminal index ranges in this table are presented in the standard industry format, although there are minor differences between the trait composition of the Signet Limousin Beef Value index and the ABRI Terminal indices of the other three breeds. The regressions suggest that there is greater value attached to bulls with higher index values. This analysis would suggest that genetic breeding values and recorded weights do play a part in purchasing decisions, although phenotypic selection remains a key element in bull-buying strategy in practice. Unlike the dairy sector, there are no formal structural soundness evaluations of pedigree beef cattle in the United Kingdom. It is therefore left to the judgement of the purchaser as to whether an animal is sufficiently sound to carry out its breeding roles, and deliver its genetic merit effectively.

Utility of BCMS as a data source

The BCMS database provided valuable information regarding breed use in the national beef herd. Records of dead animals were particularly useful in investigating the prime slaughter population, and it was possible to make estimates of breeding animal numbers, which triangulated reasonably well with other information sources. Greater recording of sire identification numbers by BCMS users would considerably enhance the commercial and research potential of this information source. In addition, tighter adherence to breed-coding protocol would greatly improve the data quality, removing the need for user interpretation of actual breed.

This issue can be overcome, at the cost of effort and accuracy, by taking into account the breed codes in the animals' ancestry. In doing this, it is possible to interpret the data, and produce a more valid estimate of breed proportions and genetic influence. However, BCMS has the potential to become the database of choice for monitoring of UK cattle genetic resources, with only minor adjustments to animal-recording protocol.

Conclusion

This study has provided the first population-wide evidence of the breed composition of UK beef cattle. Cross-breeding has been shown to be the overwhelming approach in suckler herds, in sharp contrast to the dominance of pure-bred pedigree breeding in the selection of NS sires. Importantly, it has been established that dairy genes continue to play a large role in the beef herd. The opportunity now exists to use the information provided in this study to effectively inform decision making regarding the make-up of genomic training populations.

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References

Allen D 1990. Planned beef production. BSP Professional Books, Oxford, UK.

Amer PR, Crump R and Simm G 1998. A terminal sire selection index for UK beef cattle. Journal of Animal Science 67, 445–454.

Amer PR, Niewhof GJ, Pollott GE, Roughsedge T, Connington J and Simm G 2007. Industry benefits from recent genetic progress in sheep and beef populations. Animal 1, 1414–1426.

BASCO 2010. UK animal registration numbers. Retrieved January 25, 2010, from http://www.egenes.co.uk/bascosearchbeef/

Bishop S and Woolliams JA 2004. Genetic approaches and technologies for improving the sustainability of livestock production. Journal of the Science of Food and Agriculture 84, 911–919.

British Blue Cattle Society (BBCS) 2009. Yearbook 2009. BBCS, Penrith, UK.

British Charolais Cattle Society (BCCS) 2009. Yearbook 2009. BCCS, Stoneleigh, UK.

British Cattle Movement Service (BCMS) 2009. Cattle keeper's handbook, version 3. BCMS, Workington, UK.

British Limousin Cattle Society (BLCS) 2006. Studbook and factfinder 2006. BLCS, Stoneleigh, UK.

British Limousin Cattle Society (BLCS) 2009. Studbook and factfinder 2009. BLCS, Stoneleigh, UK.

Breedplan 2010. UK animal registration numbers. Retrieved January 25, 2010, from http://breedplan.une.edu.au/

Craven JA and Kilkenny JB 1976. The structure of the British cattle industry. In Principles of cattle production (ed. H Swan and WH Broster), pp. 1–37. Butterworths, London, UK.

Defra 2004. June survey of agriculture and horticulture. Defra, London, UK.

Defra 2006. Agriculture in the United Kingdom. Defra, London, UK.

Defra 2008a. Agriculture in the United Kingdom. Defra, London, UK.

Defra 2008b. The cattle book 2008. Defra, London, UK.

Defra 2010. UK slaughter statistics. Retrieved February 1, 2010, from http://statistics.Defra.gov.uk/esg/slaughterns.htm

Edwards J, Jobst D, Hodges J, Leyburn M, O'Connor LK, Macdonald A, Smith GF and Wood P 1966. The Charolais report. Milk Marketing Board, Thames Ditton.

Eriksson S, Nasholm A, Johansson K and Philipson J 2004. Genetic relationships between caving and carcass traits for Charolais and Hereford cattle in Sweden. Journal of Animal Science 82, 2269–2276.

Gibbs D, Holloway L, Gilna B and Morris C 2009. Genetic techniques for livestock breeding: restructuring institutional relationships in agriculture. Geoforum 40, 1041–1049.

Hall JG and Clutton-Brock J 1989. Two hundred years of British livestock. Craft Print, Singapore.

Keeble M 2004. Limousin, the breed, the people, the story. Keeble, Ripon, UK.

Lowman BG 1997. Description of the UK beef industry, structure and production systems. Cattle Practice 5, 145–147.

Lowman B 1998. The past, present and future for UK suckler herds. Cattle Practice 6, 155–161.

MAFF 1977. Limousin and Simmental tests steering committee final report. MAFF, London.

McGowan M 2006. Enhancing the efficiency of natural delivery of improved genetics into beef and dairy herds. Cattle Practice 14, 33–36.

Meat and Livestock Corporation (MLC) 1990. UK meat and livestock yearbook. MLC, Milton Keynes, UK.

Office of Fair Trading (OFT) 2004. Anticipated acquisition by Genus plc of Supersires. Fleetbank House, London, UK.

Ozkutuk K and Bichard M 1977. Studies of pedigree Hereford cattle breeding. Animal Production 24, 1–13.

Penny CD, Faulkner G, Boreland J, Doyle B, Wilson A, Gibson D and Ballard D 2001. A survey of longevity and reasons for culling in UK beef stock bulls. Cattle Practice 9, 55.

Pullar D 1998. Breeding strategies for heifer replacements for the suckler herd. Cattle Practice 6, 165–168.

Riddell I 2005. Single farm payment: impact on the UK beef industry. Cattle Practice 13, 41–44.

Roughsedge T, Amer PR, Thompson R and Simm G 2005. Development of a maternal breeding goal and tools to select for this goal in UK beef production. Animal Science 81, 221–232.

Scottish Agricultural College (SAC) 2009. Farm management handbook. SAC, Edinburgh, UK.

Simm G 1998. Genetic improvement of cattle and sheep. Farming Press, Ipswich, UK.

Simm G, Bünger L, Villanueva B and Hill WG 2004. Limits to yield of farm species: genetic improvement of livestock (eds R Sylvester-Bradley and J Wiseman). In Yields of farmed species: constraints and opportunities in the 21st century, pp. 143–165. Nottingham University Press, Nottingham, UK.

Southgate JR, Cook GL and Kempster AJ 1982. A comparison of different breeds and crosses from the suckler herd. Animal Production 35, 87–98.

Todd DL 2007. A survey of the longevity and reasons for disposal of breeding bulls in the Northern Ireland suckler herd. BSc, University of Wales, Aberystwyth.

Appendix 1: Predicting the survival of beef- and dairy-sired dams

The objective is to calculate the probability that a randomly chosen calf has a dam that dies in the next 2 years. This calculation uses females recorded in British Cattle Movement Service (BCMS)/Scottish Agricultural College (SAC) as dying in 2008 and estimates the probability that a female will die within the average lifespan (24 months) of her prime

Table A1 *Probability of a dairy-sired dam dying within the lifespan of her prime slaughter progeny, using dairy-sired females recorded as dying in 2008 in BCMS/SAC. A full description of this calculation is described below*

Age group (months)	Number dying within age group ('000s)	Number alive at the start of age group ('000s)	Fraction of total calves assumed born to females in age group (P_1)	Fraction of females not surviving two consecutive age groups (Q_1)	Probability that a dam of randomly chosen calf dies in the next 2 years ($P_1 \times Q_1$)
24 to 35	32	446	0.189	0.175	0.033
36 to 47	46	414	0.175	0.249	0.044
48 to 59	57	368	0.156	0.321	0.050
60 to 71	61	311	0.132	0.373	0.049
72 to 83	55	250	0.106	0.420	0.044
84 to 95	50	195	0.083	0.492	0.041
96 to 107	46	145	0.061	0.545	0.033
108 to 119	33	99	0.042	0.616	0.026
120 to 131	28	66	0.028	0.697	0.019
132 to 143	18	38	0.016	0.763	0.012
144 to 155	11	20	0.008	0.900	0.008
156 to 167	7	9	0.004	1.000	0.004
168 to 179	2	2	0.001	1.000	0.001
Total	446	2363	1.000	8.746	0.466

BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College.

slaughter progeny. It is assumed that a typical dairy-sired female first calves at 24 months of age and that the average beef-sired female at 30 months of age, and that there is a stable age distribution.

Example calculation from Table A1. The total dying from 24 to 179 months of age (2 363 000) equates to an estimate of the size of the breeding population, which is similar to the national dairy breeding female herd estimate (Defra, 2008b). All these will be assumed to first breed in the period 24 to 35 months of age, and therefore the number of breeding females in row 1 is equivalent to the annual replacement rate. Of these replacements, 32 000 die before the end of the age period, leaving 414 000 females to enter the next age. Therefore, the fraction of calves born in a population from 36- to 47-month-old females, P_1, is $414/2363 = 0.175$. For a calf born to a 36- to 47-month-old female, the probability its dam dying in the next two periods, Q_1, is $(46 + 57)/414 = 0.249$.

Therefore, the sum of the product of $(P_1 \times Q_1)$ across all age periods is the probability that among calves born to dairy-sired cows, a dam of a randomly chosen calf dies in the next 2 years (0.466). The calculation in Table A2 follows a similar pattern to arrive at a probability among calves born to beef-sired cows, the probability that the dam of a randomly chosen calf dies in the next 2 years is 0.362.

Therefore, the dairy-sired dams were 1.29 (0.466/0.362) times as likely to die in the lifetime of their prime slaughter progeny as beef-sired dams.

Appendix 2: Genetic composition of the prime beef population

The breeding notation used in the following refers to the origin of the sire and the maternal grand sire (MGS), so that B × D is an animal with a beef sire and a dairy MGS. The prime slaughter population comprises offspring from B × B, B × D and D × D breeding females sired by beef and dairy bulls. It is assumed that dairy bulls are only used on D × D females. The term suckler herd refers to all the B × B and B × D females. Although BCMS/SAC provided breed information on the sire and MGS, the remaining 25% of the breed composition determined by the maternal grand dam (MGD) was required to be estimated. This was done using the gene flow diagram shown in Figure 1 and is explained below. The fraction of the genome deriving from beef bulls by natural service (NS) and artificial insemination (AI) was also considered, as this is related to the intensity of selection that is being practiced in the beef herd. This fraction was defined by tracing back the pedigree to male ancestors, so that a NS beef sire contributes 0.5 to the NS beef fraction, a NS beef MGS contributes 0.25 to the NS beef fraction, a NS beef sire to the MGD contributes 0.125 to the NS beef fraction and so on.

The calculation requires the following parameters that were obtained from BCMS/SAC, Office of Fair Trading (OFT, 2004) and Genus PLC (personal communication): S_B = proportion of beef-sired calves from NS within the suckler herd = 0.97; S_D = proportion of beef-sired calves from NS within the dairy herd = 0.38; P_{BB} = proportion of breeding females in suckler herd that is B × B = 0.56; P_{BD} = proportion of breeding females in suckler herd that is B × D = $1 - P_{BB} = 0.44$; Q_{BB} = proportion of prime slaughter population that are B × B = 0.57; Q_{BD} = proportion of prime slaughter population that are B × D = 0.32; Q_{DD} = proportion of prime slaughter population that are D × D = $1 - Q_{BB} - Q_{BD} = 0.11$. This is summarised by the gene flow in Figure 1.

Then the gene flow of beef genes via NS in the B × B female (P_1) is calculated by considering such a female as an offspring of a B × (B × B) mating and then as an offspring of a B × (B × D) mating to give $P_1 = P_{BB}(0.5S_B + 0.5P_1) + P_{BD}(0.5S_B + 0.25S_D)$ Solving for P_1 gives $P_1 = 0.7316$.

Table A2 *Probability of a beef-sired dam dying within the lifespan of her prime slaughter progeny, using beef-sired females recorded as dying in 2008 in BCMS/SAC. A full description of this calculation is described in the text*

Age group (months)	Number dying within age group ('000s)	Number alive at the start of age group ('000s)	Fraction of total calves assumed born to females in age group (P_1)	Fraction of females not surviving two consecutive age groups (Q_1)	Probability that a dam of randomly chosen calf dies in the next two years ($P_1 \times Q_1$)
30 to 41	34	246	0.156	0.240	0.037
42 to 53	25	212	0.135	0.212	0.029
54 to 65	20	187	0.119	0.214	0.025
66 to 77	20	167	0.106	0.234	0.025
78 to 89	19	147	0.093	0.265	0.025
90 to 101	20	128	0.081	0.297	0.024
102 to 113	18	108	0.069	0.269	0.018
114 to 125	11	90	0.057	0.244	0.014
126 to 137	11	79	0.050	0.291	0.015
138 to 149	12	68	0.043	0.471	0.020
150 to 161	20	56	0.036	0.625	0.022
162 to 173	15	36	0.023	0.639	0.015
174 to 185	8	21	0.013	0.619	0.008
186 to 197	5	13	0.008	0.692	0.006
198 to 209	4	8	0.005	0.625	0.003
210 to 221	1	4	0.003	0.750	0.002
222 to 233	2	3	0.002	1.000	0.002
234 to 245	1	1	0.001	1.000	0.001
Total	246	1574	1.000	10.283	0.362

BCMS = British Cattle Movement Service; SAC = Scottish Agricultural College.

Similarly, the gene flow of beef genes via AI in the B × B female (P_2) is

$$P_2 = P_{BB}\,(0.5\,(1 - S_B) + 0.5P_2) + P_{BD}\,(0.5\,(1 - S_B) + 0.25\,(1 - S_D)) = 0.1155$$

Solving for P_2 gives $P_2 = 0.1155$.

The remaining fraction is $1-0.7316-0.1155 = 0.1529$ and is gene flow from dairy breeds.

The gene flow of beef genes via NS to the prime slaughter population is then given by

$$0.5Q_{BB}S_B + 0.5Q_{BD}S_D + 0.5Q_{BB}P_{BB}P_1 + 0.5Q_{BB}P_{BD}\,(0.5S_D)$$

where the first two terms concern the flow of beef NS genes via the sires and the second two terms concern the flow from the dams. Note that prime slaughter animals that are B × D only have gene flow via NS of beef sires from their sire only, whereas D × D animals have no gene flow from beef sires. Substituting the values gives 0.4776.

Similarly, the gene flow of beef genes via AI is given by

$$0.5Q_{BB}(1 - S_B) + 0.5Q_{BD}(1 - S_D) + 0.5Q_{BB}P_{BB}P_2 + 0.5Q_{BB}P_{BD}0.5(1 - S_D)$$

and substituting values shows this to be 0.1658. Consequently, in total beef breeds contribute 0.643 and dairy breeds 0.357 of the genes in the prime slaughter population.

The dairy MGD fraction is obtained by subtracting the fractions accounted for by dairy sires and dairy MGS. Dairy sires account for $0.5Q_{DD} = 0.055$ and dairy MGS account for $0.25\,(Q_{BD} + Q_{DD}) = 0.108$, leaving 0.194 of gene flow from dairy through MGD. Of this gene flow, a fraction 0.95 will be from Holstein/Friesian (the proportion of dairy breed codes that are Holstein/Friesian in BCMS/SAC), that is, a total gene flow of 0.184 from this breed to the prime slaughter population through MGD. The remaining dairy contribution of 0.010 through MGD will be from other dairy breeds and in Table A2 is included in 'Other' breeds, whereas the remaining contribution through MGD of $0.25-0.194 = 0.056$ was then assigned pro rata to the beef breeds according to their MGS proportions.